CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE SUBFAMILY PERONICERATINAE HYATT, 1900

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(With 135 figures and 1 table)

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ABSTRACT

The systematics of the South African representatives of the subfamily Peroniceratinae are critically reviewed, with special attention to the almost simultaneously published monographs of Van Hoepen (27 July 1965) and Matsumoto (20 November 1965) who, although working independently, reached a number of similar conclusions and erected a series of genera that are shown to be synonyms. The genera and subgenera *Peroniceras (Peroniceras)* de Grossouvre, 1894, *P. (Zuluiceras)* van Hoepen, 1965, and *Gauthiericeras* de Grossouvre, 1894, include all the Zululand peroniceratids.

The present material is the richest assemblage of Peroniceratinae yet described, and it permits clarification of the limits of both inter- and intra-specific variability in the group as well as their evolution and stratigraphic distribution. Two new species are described: *Peroniceras (Zuluiceras) matsumotoi* and *Gauthiericeras albiforme.*

Subdivision and zonation of the Coniacian stage is critically reviewed as this has bearing on the systematics of the subfamily.

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INTRODUCTION

Ammonites referable to the subfamily Peroniceratinae Hyatt, 1900, occur abundantly in two main areas in Zululand, the lower Hluhluwe and the lower Mzinene rivers, while isolated specimens are known from the environs of Mtubatuba (Umkwelane Hill of earlier workers) and recent excavations for the construction of the new north–south highway that transects the region.

Peroniceratids were described by several early workers in the area, including Crick (1907), Spath (1921), Besairie (1930), Venzo (1936), and Van Hoepen (1955). In 1965 there appeared Van Hoepen's monographical study *The Peroniceratinae and allied forms of Zululand*. Unfortunately most of Van Hoepen's new species were based on single specimens, especially large individuals lacking the inner whorls. This led him to erect 1 new subfamily, 5 new genera, 2 new subgenera and 26 new species for his material. Only one previously established species was described, *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867).

In the same year as that of Van Hoepen's monograph, Matsumoto published his account of the Peroniceratinae from Hokkaido, Japan, in which he erected four new genera. Van Hoepen and Matsumoto, working independently, arrived at very similar conclusions in certain respects. Several of their taxa are synonyms, as will be shown below. Van Hoepen's work was published posthumously on 27 July 1965, four months before Matsumoto's on 20 November 1965. All these new taxa are reviewed in the present paper in order to stabilize nomenclature. In the process Van Hoepen's work is revised in the light of current systematic concepts and stratigraphic data. Species not described by Van Hoepen are also included in this review. The material at the present authors' disposal sheds some new light on the phylogeny and classification of the subfamily Peroniceratinae.

The following species from Zululand are described:

Peroniceras (Peroniceras) lepeei (Fallot, 1885)
P. (P.) tridorsatum (Schlüter, 1867)
P. (P.) subtricarinatum (d'Orbigny, 1850)
P. (P.) westphalicum (von Strombeck, 1859)
P. (P.) dravidicum Kossmat, 1895
P. (Zuluiceras) zulu van Hoepen, 1965
P. (Z.) rarum van Hoepen, 1965

P. (Z.) henniei van Hoepen, 1965
P. (Z.) undulatocarinatum van Hoepen, 1955
P. (Z.) modestum van Hoepen, 1965
P. (Z.) matsumotoi sp. nov.
P. (Z.) cf. *aberlei* (Redtenbacher, 1873)
P. (Z.) bajuvaricum (Redtenbacher, 1873)
Gauthiericeras obesum van Hoepen, 1955
G. listeri (van Hoepen, 1965)
G. album (van Hoepen, 1965)
G. albiforme sp. nov.
G. libertae van Hoepen, 1955

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

BMNH	British Museum (Natural History), London.
EMP	École des Mines, Paris, now in the Université Claude Bernard, Lyon
GG	Laboratoire de Géologie, Grenoble
GPIB	Geologisches und Paläontologisches Institut der Universität, Bonn
LL	Oberösterreichisches Landesmuseum, Linz
MNHP	Muséum d'Histoire Naturelle, Paris
NMB	National Museum, Bloemfontein (presently in the collections of the South African Museum)
OUM	Oxford University Museum
SAM	South African Museum, Cape Town
SAS	South African Geological Survey, Pretoria
SP	Collections of the Sorbonne, Paris, now in the Université Pierre et Marie Curie

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); fuller descriptions of these localities are deposited in the Department of Palaeontology, British Museum (National History), London; South African Geological Survey, Pretoria; and South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions are given in millimetres:
D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. R indicates ratio of umbilical to ventrolateral tubercles.

Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916) reviewed and discussed by Kullman & Wiedmann (1970) is followed here:
I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

CONIACIAN STRATIGRAPHY AND CORRELATION

Introduction

The subfamily Peroniceratinae is predominantly Coniacian and members of the group provide a basis for subdivision and correlation of the stage. Present subdivision of the stage is in a state of chaos as was made painfully apparent by Matsumoto's (1981) recent review of Coniacian biostratigraphy. Some workers use only Lower and Upper Coniacian substages, others Lower, Middle and Upper, with no clear indication as to how these two schemes are related. The same species are recorded from the 'Lower' Coniacian of one region and the 'Upper' Coniacian of another so that the ranges of taxa appear to be anomalous. Zonal nomenclature is similarly confused.

Kennedy (in press) has reviewed the early history of subdivision of the Coniacian in France, and proposed a revised zonation and subdivision into substages as summarized below.

Zonation in the type region

The Coniacian stage was introduced by Henri Coquand in 1857 as the lowest division of D'Orbigny's Senonian stage, introduced in 1842–3. It has passed into the literature as a universally applied division of the Upper Cretaceous. The standard zonation of the stage is based on ammonites and is the twofold division of De Grossouvre (1889, 1901) who recognized a lower *Barroisiceras* ['*Barroisia*'] *haberfellneri* Zone and an upper *Paratexanites* ['*Mortoniceras*'] *emscheris* Zone on the evidence of sequences in Aquitaine and Touraine in France. These zones have been universally accepted as standard zones for the Coniacian and were adopted by the 1959 *Colloque sur le Crétacé supérieur français* (Dalbiez 1960), in the *Treatise* (Wright 1957), and by Séronie-Vivien (1972) in her definitive revision of the stratotype, among many others. Yet already in 1947 Basse has pointed out that the *Barroisiceras haberfellneri* of De Grossouvre was based on a misinterpretation of Von Hauer's species, and that the French material all belonged to a distinctive form which she named *Reesideoceras gallicum* Basse, 1947 (a synonym of *Ammonites petrocoriensis* Coquand, 1859), although nevertheless referring to a '*haberfellneri*' Zone in some of her later works. True *Barroisiceras* does not occur in France, indeed, there is no good evidence that the species *B. haberfellneri* actually occurs in the Coniacian. Similarly with the *Paratexanites emscheris* Zone, the index species does not occur in France.

Confusion is not limited to nomenclature. Collignon (e.g. 1960) used the *haberfellneri–emscheris* standard in his early works, and developed a threefold zonation in Madagascar, with zones of *Peroniceras dravidicum* (oldest), *Kossmaticeras theobaldianum* and *Barroisiceras onilahyense*, and *Prionocycloceras guyabanum* and *Gauthiericeras margae* (youngest). In 1979 Collignon *et al.* recognized a sequence of three zones in the Coniacian of the Beausset Basin (Var, France): *Peroniceras tricarinatum* (oldest), *Barroisiceras haberfellneri*, and *Gauthiericeras margae* (youngest), although the middle zone was not proven by ammonites. Robaszynski *et al.* (1980) recognized a *Peroniceras tridorsatum* Zone at the base of the Coniacian in the Boulonnais, France (with, however, only eight specimens of the genus *Peroniceras* from the area), and French textbooks now cite a standard sequence of *tricarinatum–haberfellneri–margae* Zones despite the fact that *haberfellneri* does not occur in France.

In those areas where a faunal sequence can be determined, *Forresteria (Harleites) petrocoriensis* (Coquand, 1859)—the *Barroisiceras haberfellneri* of authors—always precedes *Peroniceras* species and marks the base of the Coniacian in the type area (Kennedy, Wright & Hancock 1983; Kennedy in press). Yet more recently, Matsumoto (in Matsumoto *et al.* 1981) proposed as standard zones for the European Coniacian a sequence of *Peroniceras tricarinatum* Zone (below) and *Protexanites bourgeoisi* Zone (above) on the basis of what could be gleaned from the literature.

Ammonites are generally very rare in the Coniacian of France (and indeed most of north-western Europe), and only five areas, the Aquitaine Basin, a small area in Touraine in the southern Paris Basin, a few square kilometres of outcrop around Dieulefit (Drôme), the Beausset Basin (Var), and the environs of Rennes-les-Bains in the Corbières (Aude), have yielded ammonites in any numbers. In their revision of the Craie de Villedieu, Jarvis *et al.* (1983) do not mention new records of Coniacian ammonites around Villedieu-le-Château, the most famous Coniacian ammonite locality in France. In spite of these difficulties, the French succession provided Kennedy with the basis for the following subdivision of the Coniacian:

Lower Santonian	*Texanites gallicus* Zone (provisional)
Upper Coniacian	*Paratexanites serratomarginatus* Zone *Gauthiericeras margae* Zone
Middle Coniacian	*Peroniceras (Peroniceras) tridorsatum* Zone
Lower Coniacian	*Forresteria (Harleites) petrocoriensis* Zone
Upper Turonian	*Subprionocyclus neptuni* Zone

Details are as follows:

1. *Forresteria (Harleites) petrocoriensis* Zone

The base of the zone and the Coniacian stage are marked by the appearance of the index species, specimens of which occur only centimetres above the regional hardground or discontinuity surface that separates basal Coniacian sands and marls and underlying Turonian rudistid limestones in Aquitaine. Other ammonites are rare, with only single specimens of *Scaphites (Scaphites)* cf. *meslei* de Grossouvre, 1894, *Metatissotia desmoulinsi* (de Grossouvre, 1894), and *M. nanclasi* (de Grossouvre, 1894). This is the fauna of Arnaud's (1877) Assize K of the Aquitaine sequence.

2. *Peroniceras (Peroniceras) tridorsatum* Zone

The base of the zone is marked by the appearance of diverse *Peroniceras (Peroniceras)* species. The fauna of this zone is widely recorded in Arnaud's Assize L^1 in Aquitaine and is marked by *P. (P.) tridorsatum* (Schlüter, 1867) and other *Peroniceras (Peroniceras)* species with rarer *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). Other ammonites are *Onitshoceras? ponsianum* (de Grossouvre, 1894), *Tongoboryceras* sp. nov., *Placenticeras fritschi* de Grossouvre, 1894, *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894), *Gauthiericeras? boreaui* (de Grossouvre, 1894), *Tissotia redtenbacheri* (de Grossouvre, 1894), *Metatissotia slizewiczi* (de Grossouvre, 1894), *Metatissotia ewaldi* (von Buch, 1847), *Metatissotia nodosa* (Hyatt, 1904), *Tissotioides haplophyllus* (Redtenbacher, 1873), *Scaphites meslei* (de Grossouvre, 1894), *Otoscaphites arnaudi* (de Grossouvre, 1894), and nodose *Baculites*.

Sufficient of these ammonites occur together at single localities to indicate that a single fauna is present, but the evidence from the old collections is not unequivocal. More recent collecting showed *Peroniceras (Zuluiceras) bajuvaricum, Metatissotia ewaldi*, and *Scaphites (Scaphites) meslei* occurring together at Antignac (Charente-Maritime), but suitable outcrops are now rare in Aquitaine.

Further evidence for the composition of the *P. (P.) tridorsatum* Zone fauna in France comes from Dieulefit in Drôme, where the ammonite fauna includes many forms known only from L^1 in Aquitaine. Species in common are *P. (P.) tridorsatum, P. (Zuluiceras) bajuvaricum, Metatissotia robini, Tissotioides haplophyllus*, and *S. (Scaphites) meslei*, with as additional elements *Peroniceras (P.) lepeei* (Fallot, 1885), *P. (P.) westphalicum* (von Strombeck, 1859), *P. (Zuluiceras) isamberti* (Fallot, 1885), and *Scalarites* sp.

The association from the Marnes de Ceyreste in the Beausset Basin, Var, also suggests that the assemblage represents a single zonal fauna with the co-occurrence of *Peroniceras (P.) subtricarinatum, Parapuzosia (Parapuzosia)* sp., *Placenticeras* sp., *Forresteria (Forresteria) alluaudi* (Boule, Lemoine and Thévenin, 1907) *Scaphites (Scaphites) meslei* and *Otoscaphites arnaudi*.

3. *Gauthiericeras margae* Zone

The base of the zone is marked by the appearance of *Gauthiericeras margae* (Schlüter, 1867) and *G. nouelianum* (d'Orbigny, 1850). Also present are *G. ?boreaui* (de Grossouvre, 1894), which ranges from below, *Tridenticeras* sp., and nodose *Baculites*.

The position of the zone is unequivocally demonstrated by specimens of *G. margae* from Arnaud's (1877) Assize L^2 in Aquitaine, and the record from the middle part of the Grès de Baguier of the Beausset Basin (Collignon *et al.* 1979).

4. *Paratexanites serratomarginatus* Zone

The base of the zone is marked by the appearance of the index species. Other elements of the assemblage that are restricted to the zone in France are *Protexanites (Protexanites) bontanti* (de Grossouvre, 1894), *Placenticeras semiornatum* (d'Orbigny, 1850), *Phlycticrioceras trinodosus* (Geinitz, 1850), and nodose *Baculites*. *Protexanites (P.) bourgeoisi* (d'Orbigny, 1850) ranges from below.

This is the fauna of Bed 4 of the Craie de Villedieu in Touraine (Kennedy in press). Its position is indicated by its occurrence above the condensed Calcaires Durs, which contains *Gauthiericeras margae* there, by the index species and *Protexanites (Protexanites) bourgeoisi* occurring very high in the Coniacian of northern Aquitaine, and by the index occurring above *G. margae* in the Beausset Basin in Var.

5. *The Coniacian–Santonian boundary in France*

At Javrezac (Charente), a locality mentioned by Coquand as a type section for both Coniacian and Santonian stages, the boundary is easily drawn at a hardground between glauconitic limestones of the Coniacian below and marls of the Santonian above. Defining this boundary by using ammonites is much more difficult. The precise position of ammonites within the lower part of the Santonian—Arnaud's assize M^1—is poorly documented, and ammonites are very rare indeed. De Grossouvre (1894) recorded *Paratexanites* ['*Mortoniceras*'] *serratomarginatus* (Redtenbacher, 1873) from both the Coniacian and Lower Santonian; in 1901 he decided that the Coniacian specimens all belonged to *P.* ['*Mortoniceras*'] *emscheris* (Schlüter, 1876) and that *P. serratomarginatus* was exclusively Santonian. He never illustrated Santonian *serratomarginatus*, and none survive in museum collections that can be attributed to Arnaud's M^1. Indeed, later work has shown that *P. serratomarginatus* and *P. emscheris* are not synonyms and are both from high in the Coniacian (Wiedmann 1979; Kennedy, Klinger & Summesberger 1981). De Grossouvre (1901) also indicated in a table that *Protexanites* ['*Mortoniceras*'] *bourgeoisi* (d'Orbigny, 1850) also extended into the lower part of the Santonian, but made no mention of this in the text and no specimens from M^1 survive.

Far more widely recorded is *Texanites texanus* (Römer, 1852), and this was taken as the index of the lower zone of the Santonian by De Grossouvre. Collignon (1948) correctly interpreted Römer's species (excluding all European records), which he referred to two distinct varieties, regarded by subsequent workers as either subspecies or separate species. Material from M^1 in Aquitaine (De Grossouvre 1894: 80, pl. 16 (figs 2, 4)) was referred to the variety *gallica* Collignon, 1948; the two figured syntypes are actually from M^2 at Niel-le-Virouil (Charente-Maritime). The only other specimens seen from Aquitaine are two specimens labelled *Ammonites coniaciensis* Coquand, 1857, in the École des Mines Collection ex Boucheron Collection (now in the collections of the Université Claude-Bernard, Lyons) from La Valette (Charente), a locality referred to

Assize L^2 by Arnaud, and a specimen in the Sorbonne Collections ex Toucas Collection (now in the Université Pierre et Marie Curie, Paris) from M^1, at Rentes, Cognac. This specimen is a crushed *Texanites (Texanites)* sp.

Apart from texanitids, there are poorly preserved *Placenticeras* from L^1 in the Arnaud Collection and records of *Baculites incurvatus* (Dujardin, 1837) (e.g. De Grossouvre 1901).

The conclusion is that it is not possible to define the base of the Santonian in ammonite terms in Aquitaine with any great confidence. Only from occurrences elsewhere in France e.g. Provence (Fabre-Taxy 1963) and the Corbières (Collignon & Bilotte 1983) is it possible to suggest that the appearance of *Texanites sensu stricto* is the best marker for the base of the stage, and even then the name of the zone is uncertain—the fauna may be that of De Grossouvre's *T. texanus* Zone, but the correct name for the European '*texanus*' is unresolved.

The Zululand succession

Kennedy & Klinger (1975) presented a series of working subdivisions of the Zululand Coniacian. These were not intended to be taken as zonal divisions but as a working framework only until such time as the taxonomic revisions needed to formulate a proper zonation were complete. The position has still not been achieved, but fuller faunal lists can now be given (see below). These lists included only those species known to be definitely from particular divisions. In the Upper Coniacian in particular, there are many specimens (especially in Van Hoepen's collection) collected loose from fields and hillslopes along the Hluhluwe and Mzinene rivers that may be from Coniacian IV or V (previously recorded as 'Coniacian IV–V', e.g. by Klinger & Kennedy (1980), which misleadingly suggested that the species ranged through these divisions).

Coniacian I

Gaudryceras cf. *varagurense* Kossmat, 1895, *Pachydesmoceras denisonianum* (Stoliczka, 1865), *Pachydesmoceras* sp., *Kossmaticeras (Kossmaticeras) theobaldianum theobaldianum* (Stoliczka, 1865), *K. (K.)* aff. *theobaldianum crassicostatum* Collignon, 1954, *Placenticeras kaffrarium* Etheridge, 1904, and *Didymoceras (Didymoceras) indicum* (Stoliczka, 1865). Of this assemblage, only *Kossmaticeras (K.) theobaldianum* provides indisputable ammonite evidence for a Coniacian date.

Coniacian II

Gaudryceras varicostatum van Hoepen, 1921, *Parapuzosia*(?) *donlisteri* (van Hoepen, 1968), *Kossmaticeras (Kossmaticeras) theobaldianum crassicostatum* Collignon, 1954, *K. (K.) jonesi* Collignon, 1965, *Placenticeras kaffrarium* Etheridge, 1904, *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867), *P. (P.) lepeei* (Fallot, 1885), *P. (P.) westphalicum* (von Strombeck, 1859), *P. (P.) dravidicum* Kossmat, 1895, *P. (Zuluiceras)* cf. *aberlei* (Redtenbacher, 1875), *P. (Z.) bajuvaricum* (Redtenbacher, 1873), *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), *F. (F.)* cf. *hobsoni* (Reeside, 1932), *F. (F.) madagascariensis* (Collignon, 1965), *Yabeiceras orientale* Tokunaga & Shimizu, 1926, *Y.* cf. *orientale, Y. transiens* Kennedy, Wright & Klinger, 1983, *Y. ankinatsyense* Collignon, 1965, *Y. costatum*, Collignon, 1965, *Y. manasoaense* Collignon, 1965, *Y.* aff. *manasoaense, Y. crassiornatum* Kennedy, Wright & Klinger, 1983, nodose *Baculites, Scaphites (Scaphites) meslei* de Grossouvre, 1894, and *Otoscaphites arnaudi* (de Grossouvre, 1894).

Coniacian III

Placenticeras kaffrarium Etheridge, 1904, *Peroniceras (Peroniceras) lepeei* (Fallot, 1885), *P. (P.) tridorsatum* (Schlüter, 1867), *P. (P.) dravidicum* Kossmat, 1895, *P. (Zuluiceras)* cf. *aberlei, P. (Z.) bajuvaricum,* nodose *Baculites, Scaphites (Scaphites) meslei* de Grossouvre, 1894, and *Otoscaphites arnaudi* (de Grossouvre, 1894).

Coniacian IV

Peroniceras (Zuluiceras) zulu van Hoepen, 1965, *P. (Z.) rarum* van Hoepen, 1965, *P. (Z.) modestum* van Hoepen, 1965, *P. (Z.) matsumotoi* sp. nov., *P. (Z.) henniei* van Hoepen, 1965, *P. (Z.) undulatocarinatum* (van Hoepen, 1955), *Gauthiericeras obesum* van Hoepen, 1955, *G. listeri* (van Hoepen, 1965), *G. albiforme* sp. nov., *G. planulatum* van Hoepen, 1955, *G. libertae* van Hoepen, 1955, *G. album* (van Hoepen, 1955), *Protexanites (Protexanites) cynci* (van Hoepen, 1968), *Paratexanites australis* Klinger & Kennedy, 1980, *P. aff. P. emscheris* (Schlüter, 1876) (*Protexanites* and *Paratexanites* are very rare *in situ* in Coniacian IV), and nodose *Baculites.*

Coniacian V

Protexanites (Protexanites) cynci (van Hoepen, 1968), *Paratexanites australis* Klinger & Kennedy, 1980 (many loose *Protexanites* and *Paratexanites* are probably from Coniacian V, outcrops of which are poor), *Pseudoschloenbachia* aff. *primitiva* Collignon, 1965, and feebly nodate and non-nodate *Baculites.*

Santonian I

The base of the Santonian is taken at the appearance of diverse *Texanites* species.

Correlation of the Zululand succession with that recognized by Kennedy in France is rendered difficult by the low diversity of the ammonite faunas of the European Lower Coniacian *Forresteria (Harleites) petrocoriensis* Zone and Coniacian I in Zululand, plus the difficulty of finding *in situ* faunas in Coniacian V.

Coniacian II and III correlate with the Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone, having many elements in common. Coniacian I may be equivalent to the Lower Coniacian *F. (H.) petrocoriensis* Zone. It is equally possible (at least on the ammonite evidence) that this is absent, with early Coniacian time represented in the sub-Coniacian unconformity. In the latter case the sparse fauna of this division could simply be an impoverished Middle Coniacian assemblage. Only evidence from other groups can resolve this problem.

The base of Coniacian IV in Zululand is to be correlated with the base of the European Upper Coniacian *Gauthiericeras margae* Zone on the basis of the close similarities between the *Gauthiericeras* in the two regions. The presence of several (albeit rare) *Protexanites* and *Paratexanites* species may indicate that the top of Coniacian IV extends into the base of the succeeding *Paratexanites serratomarginatus* Zone, but *P. zeilleri* (de Grossouvre, 1894) is a pre-*P. serratomarginatus* Zone species (the holotype is from the condensed Calcaires Durs de la Ribochère (*petrocoriensis* to *margae* Zones)), and there are records of rare *Protexanites* below the *P. serratomarginatus* Zone.

Coniacian V in Zululand is probably to be correlated with the European Upper Coniacian *P. serratomarginatus* Zone, but the paucity of ammonite species and poor exposure do not permit certainty that it does not extend into the lowest Santonian. While the appearance of *Texanites* in numbers marks the Lower Santonian in both areas, it is still not clear if this is, indeed, the base of the stage.

Madagascar

Coniacian faunas from Madagascar are the richest known, and are described in works by Boule, Lemoine & Thévenin (1906–7), Collignon (1931, 1948, 1954, 1965), Besairie (1936), and Basse (1927, 1931, 1947, etc.).

Well illustrated as the faunas are, their stratigraphic distribution presents many problems and detailed successions are generally lacking.

In 1960 Collignon provided a threefold zonation maintained in his later works:

Lower Santonian	*Texanites oliveti* Zone
Upper Coniacian	*Prionocycloceras guyabanum* and *Gauthiericeras margae* Zone
Middle Coniacian	*Kossmaticeras theobaldi* and *Barroisiceras onilahyense* Zone
Lower Coniacian	*Peroniceras dravidicum* and *P. subtricarinatum* Zone
Upper Turonian	*Romaniceras deveriai* and *Coilopoceras requieni* Zone

In understanding these successions, the faunas from individual localities are more revealing than those of the synthetic accounts.

In the Diego Basin Besairie & Collignon (1972: 49) note that the Senonian consists of sandstones and sandy marls with several limestone beds, and that there are no vertical successions. Faunas recorded indicate both Middle and Upper Coniacian (in the sense used here) to be present.

In the Majunga Basin the same authors record only a fauna with *Barroisiceras* from Antsira. The assemblage consists of *Barroisiceras onilahyense* Basse, 1947, *Lewesiceras beantalyense* Collignon, 1952, and *Peroniceras* sp.

In the Morondava Basin Besairie & Collignon (1972: 249) recognize Coniacian with *Peroniceras rousseauxi* de Grossouvre, 1894, and *Lewesiceras tongoboryense* Collignon, 1952, above post-Lower Turonian basalts. The same relationship is observed between Demoka and Manambolo, with '*Lewesiceras*' *tongoboryense* Collignon, 1952, *Peroniceras rousseauxi* De Grossouvre, 1894, and '*Hyporbulites*' *masiaposensis* Collignon, 1956, east of Bevitsika, and *Peroniceras* sp. *Gaudryceras analabense* Collignon, 1956, and *Tetragonites wieli* Collignon, 1956, north-west of Bemonta. At Ankotrofotsy, a 7–8 m sequence of marls and reefal limestones resting on basalt yielded (Hourcq 1950) *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), *Kossmaticeras (Kossmaticeras) recurrens* Kossmat, 1897, *Oxybeloceras, Phylloceras (Hypophylloceras), Gaudryceras, Puzosia*, and *Pachydiscus*. The first of these faunas was regarded as Lower Coniacian, but the presence of *Peroniceras* at the first two localities and *Forresteria (F.) alluaudi* at the third all indicate the Middle Coniacian *Peroniceras (P.) tridorsatum* Zone as defined here.

In the centre of the Morondava Basin the Turonian forms a continuous strip from Manambolo to Andranomena (Besairie & Collignon 1972) with Lower Turonian containing *Fagesia*, and an Upper Turonian containing *Romaniceras*. The facies is mixed, with coarse red sandstones, sometimes with silicified wood.

At Masiaposa, 3 km west of Antsarona, there is a rich fauna with (among other stratigraphically unimportant taxa) *Romaniceras (Romaniceras) deverianum* (d'Orbigny, 1841), *Coilopoceras requienianum altesselata* Collignon, 1965, *Kossmaticeras (Kossmaticeras) recurrens* Kossmat, 1897, *Subprionocyclus neptuni* (Geinitz, 1850), *Subprionocyclus casterasi* Collignon, 1965 (? = *S. normalis* Anderson, 1958), *Masiaposites* spp., and *Hourcquia* spp.

The Turonian and Coniacian are separated by a basaltic interlude, succeeded by 'Coniacien Inférieur'; between Manambolo and Tsiribihina, there are approximately 20 m of yellow-grey marls with sandy limestones, yielding many ammonites referred to the *Peroniceras dravidicum* Zone. Important taxa are *P. (Peroniceras) dravidicum* Kossmat, 1895, *P. (P.) subtricarinatum* (d'Orbigny, 1850), *P. (P.)* cf. *tridorsatum* (Schlüter, 1867), *P. (P.) westphalicum* (von Strombeck, 1859), *P. (P.) moureti* de Grossouvre, 1894, *P. (Zuluiceras)* aff. *czoernigi* (Redtenbacher, 1873), *P. (P.) besairiei* van Hoepen, 1965, *P. (P.) tenue* van Hoepen, 1965, *P. (P.) guerini* Collignon, 1965, '*Lewesiceras*' spp., *Yabeiceras menabense* Collignon, 1965, and *Y. ankinatsyense* Collignon, 1965 (see full list, by locality, in Besairie & Collignon 1972: 283).

Above, the 'Coniacien Moyen' and 'Supérieur' are represented by 30 m of yellow marls, with the Zone à *Kossmaticeras theobaldi* et *Barroisiceras onilahyense* yielding: *Barroisiceras onilahyense* Basse, 1947, *Subbarroisiceras mahafalense* Basse, 1946, *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), *F. (F.) madagascariensis* (Collignon, 1965), *Yabeiceras bituberculatum* Collignon, 1965, *Y. costatum* Collignon, 1965, *Y. ankinatsyense* Collignon, 1965, *Y. magnumbilicatum* (Basse, 1946), *Kossmaticeras (Kossmaticeras) theobaldianum* (Stoliczka, 1865) and other species, plus numerous other forms listed by Besairie & Collignon (1972: 283). The 'Coniacien Supérieur' Zone à *Prionocycloceras guyabanum* et *Gauthiericeras margae* yields only the index species and long-ranging taxa (Besairie & Collignon 1972: 284).

The base of the Santonian *Texanites oliveti* Zone is marked by the appearance of the index species and many other taxa.

These observations indicate that there is no ammonite evidence for the Lower Coniacian *F. (H.) petrocoriensis* Zone of the European standard, and that the 'Coniacien Moyen' *Peroniceras (P.) dravidicum* Zone is equivalent to part of the European *P. (P.) tridorsatum* Zone. The paucity of common elements between the succeeding *B. onilahyense* and *K. (K.) theobaldi* Zone and European faunas makes comparison difficult, but *Forresteria (F.) alluaudi* is a common species, suggesting that the zone is also Middle Coniacian and equivalent to part of the *P. (P.) tridorsatum* Zone.

Comparisons with Zululand are close but pose problems. Whereas the peroniceratids of the Madagascan *P. (P.) tridorsatum* Zone indicate correlation with Coniacian II and III, the absence of *Forresteria (Forresteria)* in the *P. (P.) tridorsatum* Zone in Madagascar but its presence in the succeeding *Barroisiceras onilahyense–Kossmaticeras theobaldi* Zone is the reverse of the order seen in Zululand where this genus occurs with *Peroniceras* in Coniacian II but is absent in Coniacian III, with *Peroniceras* persisting.

There is insufficient evidence to resolve this apparent inconsistency.

The fauna of the *Prionocycloceras guyabanum–Gauthiericeras margae* Zone has little in common with European faunas; the one fragment of *G. margae* figured by Collignon (1965, pl. 435 (fig. 1798)) is so poor as to be indeterminate from the figure. Correlation with the *G. margae* Zone is suggested. Correlation with Zululand is easier: there are *Prionocycloceras* species common to this zone and Coniacian IV.

Japan

Matsumoto (1981) has presented the most recent review of the sequence of ammonite faunas in the Japanese Coniacian, the chief sections being in Hokkaido, Kyushu, and Shikoku. Interpretation of the sequence is often difficult due to complex tectonics and the general rarity of ammonites.

A twofold division based on inoceramids is recognized, with a zone of *Inoceramus uwajimensis* below and *I. mihoensis* above. These species are stratigraphically separated in some areas (e.g. the Ikushumbets, Futaba, and Orogawa areas), but elsewhere (e.g. the Obira area of Hokkaido) they overlap, with *I. mihoensis* being the later species to appear.

Potentially important species for long-term correlation from these divisions are as follows:

Inoceramus uwajimensis Zone

Nowakites mikasaensis Matsumoto, 1979, *Prionocycloceras wrighti* Matsumoto, 1971, *P. sigmoidale* Matsumoto, 1965, *Prionocycloceras* sp. aff. *P. lenti* (Gerhardt, 1897), *Ishikariceras binodatum* Matsumoto, 1965, *Paratexanites serratomarginatus* (Redtenbacher, 1873), *Barroisiceras onilahyense* Basse, 1947, *Pseudobarroisiceras nagaoi* Shimizu, 1932, *Barroisiceras (Basseoceras) inornatum* Matsumoto, 1970, *F. (Muramotoa) yezoensis* Matsumoto, 1970, *F. (M.) muramotoi* Matsumoto, 1970, *Yabeiceras orientale* Tokunaga & Shimizu, 1926, '*Harleites* cf. *harlei* (de Grossouvre, 1894)' (apparently a feebly ornamented *Forresteria (F.) alluaudi*), and *Hourcquia hataii* Hashimoto, 1973. Recorded from either this zone or that succeeding it are *Peroniceras (Peroniceras) yubarense* Matsumoto & Muramoto, 1981 (said to be a close ally of *P. (P.) besairiei* van Hoepen, 1965) and *P. (P.)* aff. *platycostatum* van Hoepen, 1955 (*P. (P.) dravidicum* Kossmat, 1895, according to the present revision).

Elements undoubtedly from this zone listed above show that it is certainly in part Middle Coniacian, equivalent to the European *tridorsatum* Zone and to Coniacian II of the Zululand sequence. There is no ammonite evidence for Lower Coniacian. The only anomalous record is of *Paratexanites serratomarginatus*, a species known only from the Upper Coniacian *P. serratomarginatus* Zone in Europe and only from the Upper Coniacian elsewhere.

The basis of the record is given in Matsumoto (1970: 260). One specimen was from a fallen nodule near the Coniacian–Santonian boundary, and a second was also collected loose in Hokkaido. The only well-localized specimen is the fragment figured by Matsumoto (1970, pl. 36 (fig. 2)) from his 'Locality IK2112, Go-no-sawa, Pombets, a tributary of the Ikushumbets', zone of *Inoceramus uwajimensis* K5 (Coniacian).

Inoceramus mihoensis Zone

Peroniceras (Peroniceras) latum Matsumoto & Muramoto, 1981 (probably *P. (P.) westphalicum*), *Sornayceras omorii* Matsumoto, 1965 (= *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873)), *P. (Z.) proteus* Matsumoto, 1965, *Paratexanites orientalis* (Yabe, 1925), and *P. mikasaensis* Matsumoto, 1970.

This assemblage appears to be in part equivalent to the European *Peroniceras (P.) tridorsatum* Zone and includes species allied to those of the *Gauthiericeras margae* and *Paratexanites serratomarginatus* zones, indicating it to be in part Middle and in part Upper Coniacian. When compared with the Zululand succession it has common (or closely comparable) species to those of Coniacian III and IV.

Texas

The Coniacian ammonite faunas of this vast region have been described by Young (1963), Wolleben (1967), and Young & Powell (1978).

The Coniacian is represented in the Austin Chalk and its correlatives. Over much of Texas east of the Pecos there is a regional break between the Austin and the underlying Eagle Ford. The base of the Austin is Coniacian (but not lowest Coniacian) in the Dallas area, but becomes progressively older when traced southwards, until it is Upper Turonian along the Rio Grande. The standard zonation proposed by Young is: *Prionocycloceras gabrielense* Zone (youngest), *Peroniceras westphalicum* Zone, and *Peroniceras haasi* Zone (oldest). Faunas of these zones are rather poor in number and species.

Peroniceras (P.) haasi Young, 1963 (less than twenty specimens) and *Coilopoceras austinense* Adkins, 1931 (Adkins 1931: 50, explanation of pl. 4), one specimen, the holotype, are from Bear Creek 'about ⅜ mile west of Marchaca', which is said to be in both Travis and Hays counties. The only precisely localized *P. (P.) haasi* specimens are fragments from '30 feet above the base of the Austin' from Williamson County, a specimen from the basal '15 feet of the Austin Chalk' on

Boudin Creek, Travis County, and the basal '20 feet of the Austin' at Watters Park, Travis County (Young 1963: 72). *Inoceramus* species collected from 2 m above the base of the Austin at Cedar Hill Scarp, Johnson County, are *Cremnoceramus deformis* (Meek, 1871) (an early form of Kauffman (OUM KT5386–9)).

According to Kauffman, Cobban & Eicher (1978), *Cremnoceramus deformis* (early form) characterizes the upper part of the lower half of the *Scaphites preventricosus* Zone of the U.S. Western Interior.

The *Peroniceras (P.) westphalicum* Zone yielded *P. (P.) westphalicum* (seven specimens) and *P. (P.) moureti* (interpreted here as *P. (P.) tridorsatum*) (two specimens). *Prionocycloceras adkinsae* Young, 1957, was inferred to be from this zone on phylogenetic grounds alone.

The *Prionocycloceras gabrielense* Zone yielded *P. gabrielense* Young, 1957 (five specimens), *P. hazzardi* Young, 1957 (the holotype plus two doubtful juveniles), *Parabevahites sellardsi* Young, 1957 (three specimens), and *Protexanites planatus* (Lasswitz, 1904) (eleven specimens). Wolleben (1967), working in Trans-Pecos Texas, added *Placenticeras colquitti* Wolleben, 1967 (two specimens), and *Prionocycloceras adkinsae* Young, 1963 (one specimen) to the *P. gabrielense* Zone assemblage.

It is concluded that the ammonites of the *Peroniceras haasi* and *P. westphalicum* Zones indicate the Middle Coniacian, and are equivalent to the European *P. (P.) tridorsatum* Zone. There is no ammonite evidence for the Lower Coniacian.

Northern Spain

A series of papers by Wiedmann (1960, 1964, 1979, 1980) and Wiedmann & Kauffman (1978) have documented the sequence of Upper Cretaceous ammonite faunas in northern Spain, building on early work by Karrenberg (1935), Ciry (1940, 1951), and others.

It is important to note that the highest Turonian ammonites, which include *Romaniceras (Romaniceras) deverianum* (d'Orbigny), are generally separated from the first Coniacian ammonites by a rudistid limestone complex that is 25 m thick at Picofrentes in the Celtiberic Ranges and 50–80 m thick in the Nela area of the Vascogotic Ranges. The succeeding Coniacian consists of sandy and glauconitic marls up to 200 m thick in the Vascogotic Ranges. Two important sections are given in detail as a basis for discussion.

Ollogoyen, Navarra (1°32′15″E 42°41′15″N)

The section consists of 110 m of grey clays and silty marls. Details are as follows (after Wiedmann 1960: 718; 1979: 177, with original nomenclature):

1. Upper part of Middle Turonian (Zone VII): more than 10 m with *Romaniceras inerme* (de Grossouvre, 1889), and *Proromaniceras pseudodeverianum* (Jimbo, 1894).
2. Upper Turonian (Zone VII): about 50 m with *Romaniceras ornatissimum* (Stoliczka, 1865), *R. (R.)* cf. *deverianum* (d'Orbigny, 1841), *Collignoni-*

ceras? sp., *Pachydesmoceras denisonianum* (Stoliczka, 1865), and *Puzosia* cf. *P. planulata* (J. de C. Sowerby, 1827).

3. Lower Coniacian (I and ?II): about 45 m with *Tissotia (Metatissotia)* cf. *robini* (Thiollière, 1848), *Reesideoceras* cf. *R. camerounens* Basse, 1947, and *Proplacenticeras* sp.

4. Middle–Upper Coniacian (Zones ?III and IV): about 50 m of massive limestones.

5. Upper Coniacian (Zone V): sandy marls and marly limestone of the Col d'Ollogoyen with *Paratexanites* cf. *P. emscheris* (Schlüter, 1876), *Gauthiericeras aberlei* (Redtenbacher, 1873), *Gaudryceras vascogoticum* Wiedmann, 1962, and *Scaphites compressus* d'Orbigny, 1842.

Terradillos de Sedano, Burgos (0°8′05″E 42°39′10″N)

1. Middle–Upper Turonian (Zones VII and VIII) massive, well-bedded limestones with *Vaccinites*.

2. Lower Coniacian (Zone I): 32 m marls and marly limestones, glauconitic sandstones and marls with *Tissotioides haplophyllus* (Redtenbacher, 1873), *T. crassus* Ciry, 1940, *Metatissotia robini* (Thiollière, 1848), *M. ewaldi* (von Buch, 1847), *Parapuzosia* cf. *P. corbarica* (de Grossouvre, 1894), to which can be added *Tongoboryceras* sp. (OUM KZ 14001) and *Scaphites meslei* (de Grossouvre, 1894) (OUM KZ 14006).

3. Lower Coniacian (Zone II): 4 m calcarenites and limestones with *Reymentoceras hispanicum* (Wiedmann, 1960) and *Protexanites bourgeoisi* (d'Orbigny, 1850).

4. Middle Coniacian (Zone III): 16 m grey marls with *Gauthiericeras vallei* Ciry, 1940, *G. margae* (Schlüter, 1867), *G. gordum* (Karrenberg, 1935), *Barroisiceras* cf. *B. sequens* (de Grossouvre, 1894), *Texasia iberiense* (Basse, 1947), *Reesideoceras* cf. *camerounense* Basse, 1947, *R.* cf. *R. nicklesi* (de Grossouvre, 1894), *Paratexanites zeilleri* (de Grossouvre, 1894), and *Scaphites* ex aff. *arnaudi* de Grossouvre, 1894.

5. Upper Coniacian (Zone IV): 12 m of brown marls with *Hemitissotia turzoi* Karrenberg, 1935, *Texasia* cf. *dartoni* Reeside, 1932, and *Protexanites* sp. nov.

6. Upper Coniacian (Zone V): 5 m of marls similar to those of Zone IV with *Hemitissotia lenticeratiformis* Wiedmann, 1978.

7. Lower Santonian (Zone I): 7,5 m of marls and 8 m of marly limestones with *Texanites hispanicus* Collignon, 1948, and *Lenticeras* cf. *lissoni* Knetchel, 1947.

8. Upper Santonian: 20 m red limestones with larger benthonic Foraminiferida.

At first sight this succession appears wholly incompatible with the sequence developed by Kennedy (in press) for the French succession. De Grossouvre (1901) had long ago recognized that the acme of Tissotidae in France occurred at least at the level of appearance of *Peroniceras*. Subsequent work has confirmed this and the following species are of the *Tissotioides haplophyllus* Zone: *T. haplophyllus* (of which *T. crassus* is a synonym (Kennedy in press)), *Metatissotia robini* and *M. ewaldi*, which are restricted to the *P. (P.) tridorsatum* Zone in France, whereas *Tongoboryceras* and *Scaphites (Scaphites) meslei* are commonest in this zone. It is concluded that the *Tissotioides haplophyllus* Zone of Wiedmann is equivalent to the *P. (P.) tridorsatum* Zone.

The only common element of the *Texanites hispanicum* Zone and the French sequence is *Protexanites bourgeoisi*. In France this is generally uppermost Coniacian, but *Protexanites* does occur low in the Upper Coniacian in Zululand.

The fauna of the *Gauthiericeras vallei* Zone presents most apparent anomalies. It does include *G. margae*, but the other recorded species of '*Gauthiericeras*' *(G. turzoi, G. gordum, G. vallei)* are all *Prionocycloceras*. So far as can be judged from large new collections, the *Prionocycloceras* at this level includes compressed, flat-sided forms as well as the depressed strongly ribbed types already noted, and *Barroisiceras iberiense* Basse (1947: 118; lectotype herein designated, the original of Basse's pl. 7 (fig. 2)) is one such compressed form; *Barroisiceras* cf. *sequens* of Wiedmann & Kauffman (1978, pl. 11 (fig. 3)) and Wiedmann (1980, pl. 11 (fig. 3)) is probably another, as may be the *Reesideoceras* cf. *camerounense* recorded from the zone. (Unpublished observations by C. W. Wright on Colombian *Prionocycloceras* show a comparable range of variation from depressed and coarsely ribbed to compressed and feebly ribbed specimens.)

Of other species noted by Wiedmann, *Paratexanites zeilleri* can be dated only as pre-*Paratexanites serratomarginatus* Zone in France, and *Otoscaphites* ['*Scaphites*'] ex. aff. *arnaudi* is impossible to assess without illustrations. *O. arnaudi* itself appears in the *P. (P.) tridorsatum* Zone. The *Gauthiericeras vallei* Zone is thus directly equivalent to the *G. margae* Zone of the French sequence.

The *Gauthiericeras turzoi* and *Hemitissotia lenticeratiformis* zones cannot be correlated with the sequences in France (or indeed elsewhere), having no described elements in common.

Romania

Szász (1981) presented the most recent review of the Coniacian succession in Romania. Two areas were investigated — the Babadag Basin (north Dobrogea) and the Cheia Valley–Vinturarita (south Carpathians). In the Babadag Basin two successive zones were recognized, a zone of *Barroisiceras haberfellneri* below and one of *Peroniceras moureti* above. In the Vinturarita region, only one zone of *Forresteria (Reesideoceras) petrocoriensis* was recognized, and equated with the *Barroisiceras haberfellneri* Zone of the Babadag Basin.

Details of the zonal assemblages are as follows:

Zone of *Barroisiceras haberfellneri*

Barroisiceras haberfellneri haberfellneri (von Hauer, 1866), *Harleites bentori* Parnes, 1964, *Yabeiceras* sp. (aff. *Yabeiceras orientale* Tokunaga & Shimizu, 1926), *Pseudokossmaticeras* sp. (sp. nov?), *Nowakites*? *macoveii* Szász, 1981, *Scaphites* ex gr. *compressus* d'Orbigny, 1842, *Gaudryceras* aff. *varagurense* Kossmat, 1891, *Gaudryceras* aff. *mite* (von Hauer, 1866), *Damesites* spp., *Austiniceras* cf. *mobergi* (de Grossouvre, 1894), *Neocrioceras (Schlueterella) kossmati* (Simionescu, 1899), and *Neocrioceras* sp. Also recorded from this level are *Harleites harlei* (de Grossouvre, 1894), *Gaudryceras denseplicatum* (Jimbo, 1894), and *Pseudokossmaticeras* ?sp. nov.

Zone of *Peroniceras moureti*

Peroniceras moureti de Grossouvre, 1894, *Peroniceras tridorsatum* (Schlüter, 1867), *Peroniceras* sp., *Nowakites carezi* (de Grossouvre, 1894), and *Puzosia* ex. gr. *orientalis* Matsumoto, 1954. Previous records from this level include *Peroniceras czoernigi* (Redtenbacher, 1873), *Peroniceras rousseauxi* de Grossouvre, 1894, *Eupachydiscus sayni* (de Grossouvre, 1894), and '*Anisoceras*' *sertum* Müller & Wolleman, 1904.

Zone of *Forresteria (Reesideoceras) petrocoriensis*

Forresteria (Reesideoceras) petrocoriensis (Coquand, 1865), *Sornayceras* aff. *omorii* Matsumoto, 1965, *Nowakites tallavignesi* (d'Orbigny, 1850), *Nowakites lemarchandi* (de Grossouvre, 1894), *Pseudokossmaticeras brandti* (Redtenbacher, 1873), *Neocrioceras (Schlueterella) kossmati* (Simionescu, 1899), *Hyporbulites* cf. *bizonatus* (Fritsch, 1872), *Gaudryceras* aff. *varagurense* Kossmat, 1895, *Gaudryceras* aff. *mite* (von Hauer, 1866), *Scaphites* ex. gr. *compressus* d'Orbigny, 1842, *Tetragonites (Epigoniceras)* sp. nov. (aff. *T. (E.) epigonum*) Kossmat, 1895, *Tetragonites*? sp., and *Puzosia* sp.

The *P. moureti* Zone is clearly equivalent to the Middle Coniacian *P. tridorsatum* Zone as used here. The *F. (R.) petrocoriensis* Zone is also part at least equivalent to the *tridorsatum* Zone (some of Szász's *F. (R.) petrocoriensis* are actually Middle Coniacian *F. (H.) nicklesi* (de Grossouvre) (e.g. Szász 1981, pl. 11 (fig. 1)). The *B. haberfellneri* Zone also presents difficulties; the only common element with faunas we have studied is the *Yabeiceras*, which suggests this zone to be Middle Coniacian.

TABLE 1

Coniacian correlation

SUBSTAGE	FRANCE	ZULULAND	MADAGASCAR	SPAIN
LOWER SANTONIAN	*'gallicus'*	I	*oliveti*	*hispanicus* ?—?—?—?
UPPER CONIACIAN	*serratomarginatus*	V	*guyabanum* et *margae*	*lenticeratiformis* *turzoi* *vallei* ?—?—?—?
	margae	IV		
MIDDLE CONIACIAN	*tridorsatum*	III + II ?—?—?—?	*theobaldi* et *onilahyense* + *dravidicum* et *subtricarinatum*	*hispanicum* + *haplophyllus*
LOWER CONIACIAN	*petrocoriensis*	? I	—	—

Conclusions

The preceding observations lead to the correlation shown in Table 1. In the following sections the terms Lower, Middle and Upper Coniacian are as used in the present discussion, and not as used by previous authors.

SYSTEMATIC PALAEONTOLOGY

Phylum **MOLLUSCA**

Class Cephalopoda Cuvier, 1797

Subclass ammonoidea Zittel, 1884

Order AMMONITIDA Hyatt, 1889

Superfamily acanthocerataceae de Grossouvre, 1894

Family **Collignoniceratidae** Wright & Wright, 1951

Subfamily Peroniceratinae Hyatt, 1900

Discussion

Wright (1957: L428–429) included four genera in the subfamily Peroniceratinae: *Prionocycloceras* Spath, 1926, *Gauthiericeras* de Grossouvre, 1894, *Peroniceras* de Grossouvre, 1894, and *Yabeiceras* Tokunaga & Shimizu, 1926. The authors follow Matsumoto (1964, 1965) in transferring *Yabeiceras* to the subfamily Barroisiceratinae and *Prionocycloceras* to the subfamily Collignoniceratinae.

Gauthiericeras, with type species *Ammonites margae* Schlüter, 1867, was erected by De Grossouvre (1894: 87) for a series of species 'dont les tours à section subquadrangulaire présentent sur leur bord externe une quille médiane très saillante: en dehors de ce caractère extérieur, les cloisons offrent aussi certaines particularités spéciales qui les placent comme formes de transition entre celles des *Mortoniceras* et celles du genre suivant, *Peroniceras*'.

Peroniceras, with type species *P. moureti* de Grossouvre, 1894, was diagnosed (De Grossouvre 1894: 93) as including a group of species presenting 'd'assez grandes affinités avec les *Mortoniceras* et les *Gauthiericeras*, mais s'en distinguant par leur bord externe orné de trois quilles et par une ligne suturale beaucoup plus découpée et plus élancée qui rapelle celle des *Stoliczkaia*: le premier lobe latéral est, comme dans ce dernier genre, assez étroit et terminé par une fourche bien nette. La troisième selle latérale a aussi son extrémité supérieure bien au-dessus de celles des deux premières.'

Concerning the suture-line of *Peroniceras* ['*Schloenbachia*'] *dravidicum*, Kossmat (1895: 190) noted that 'der erste Lateralsattel von beiden Seiten her stark eingeschnürt und von sehr zierlicher Gestalt, der zweite Lateralsattel ist nicht mehr selbständig, sondern dem ersten Lateralsattel als grosser schiefer Ast angehängt...'. Kossmat also maintained that all *Peroniceras* species possessed a similar suture-line, though not always as pronouncedly developed. In this respect he mentioned *Peroniceras czoernigi* (Redtenbacher), *P. tridorsatum* (Schlüter) and *P. moureti* de Grossouvre.

The diagnoses of *Peroniceras* and *Gauthiericeras* as given by De Grossouvre and slightly elaborated on by Kossmat remained virtually unchanged during the ensuing 60 years. In 1957 the diagnoses of *Peroniceras* and *Gauthiericeras* were given in the *Treatise* (Wright 1957: L429) as:

Gauthiericeras. 'Rather evolute; whorl section trapezoidal to subquadrate; with entire or feebly crenulate high keel bearing a distinct groove on either side; strong ribs spring at first in pairs, later usually singly, from single or double umbilical tubercles and end in strong ventrolateral tubercles.'

Peroniceras. 'Very evolute, with oval, trapezoidal or square whorl section; venter with 3 entire keels, middle one as high as others or higher; regular rounded or conical umbilical tubercles are joined to slightly larger number of similar ventrolateral ones by short straight rounded ribs; also, lateral tubercles may occur.'

Reyment (1957: 65) added a new subgenus to *Peroniceras, P. (Reginaites)*, with type species *P. (Reginaites) quadrituberculatum* Reyment, 1957. This is an evolute form with tricarinate venter but with four rows of tubercles. As the authors have previously shown (Klinger & Kennedy 1980), *Reginaites* is more appropriately referred to the subfamily Texanitinae Collignon, 1948, and is closely allied to and often homoeomorphic with *Plesiotexanites*. In addition, it seems to be restricted to the Upper Santonian and possibly the lowermost Campanian (in Zululand), rather than Coniacian as initially presumed by Reyment.

Wiedmann (1960) described a new subgenus of *Gauthiericeras, G. (Ciryella)*, type (and only) species *G. (Ciryella) vascogoticum* Wiedmann, 1960, from the 'Lower' Coniacian of Spain. As shown above, the type species is no older than Middle Coniacian. This is a widely umbilicate form with a single keel, fastigiate venter, two rows of tubercles, and a rather simple suture, in several respects intermediate between *Peroniceras* and *Gauthiericeras*, according to Wiedmann.

In 1965 this relatively simple classification, comprising four genera (or subgenera) only, was extended by the addition of a new subfamily, nine new genera and two subgenera by the independent studies of Van Hoepen and Matsumoto.

Van Hoepen's publication received a rather narrow circulation, and his diagnoses are given here in full; Matsumoto's diagnoses are summarized where appropriate.

Reiterating Kossmat's (1895: 190) views, Van Hoepen (1965: 4) defined *Peroniceras* as 'ammonites with three keels at a full-grown stage and with a suture-line which is deeply incised and of which the third lateral saddle is rooted in the inner lower corner of the second lateral saddle and which is separated from the auxiliary saddles by a more or less horizontal, sometimes deeply penetrating lobe'.

The new subgenera of *Peroniceras, P. (Zuluiceras)*, type species *P. Zuluiceras zulu* van Hoepen, 1965, and *P. (Zuluites)*, type species *P. (Zuluites) modestum* van Hoepen, 1965, were defined as follows:

P. (Zuluiceras). 'Ammonites with umbilicus narrower than in *Peroniceras* sensu stricto and whorl section more or less square in the early stages, but increasing more rapidly in height than in *Peroniceras* sensu stricto and tending to become inflated and rounded in later stages; the ribs are stronger relative to the tubercles than in *Peroniceras* sensu stricto' (Van Hoepen 1965: 9);
P. (Zuluites). 'A further development of the trend exhibited by *Zuluiceras*; distinguished from that subgenus by the still greater whorl-height and oval whorl section. Ornamentation gradually becomes weaker and eventually disappears completely.' (Van Hoepen 1965: 23).

In the new subfamily Gauthiericeratinae (ex Gauthiericeratidae van Hoepen (1955), Van Hoepen (1965) included 'ammonites with three keels at a full-grown stage of which the suture-line is little incised; the axes of the three lateral saddles and the two lateral lobes are more or less parallel; the third lateral saddle is short and high up the suture'.

Apart from the nominate genus *Gauthiericeras,* Van Hoepen included five new genera in the subfamily Gauthiericeratinae: *Andersonites*, type species *A. listeri* van Hoepen, 1965; *Fluminites,* type species *F. albus* van Hoepen, 1965; *Hluhluweoceras*, type species *H. fugitivum* van Hoepen, 1965; *Falsebayites*, type species *F. peregrinus* van Hoepen, 1965; and *Fraudatoroceras*, type species *F. besairiei* van Hoepen, 1965. With the exception of *Falsebayites*, the type species of which was based on two specimens, all the other taxa were based on single specimens. In order of pagination they were defined as follows:
Andersonites. 'Ammonites with three keels, wide umbilicus, more or less square section, very strong, straight ribs each with two tubercles, a very large shoulder tubercle and only slightly smaller umbilical tubercle' (Van Hoepen 1965: 29).
Fluminites. 'Ammonites with three keels, wide umbilicus and a section which is at first higher than broad. The ribs are strong and slightly concave forwards. They are at first close together, but later far apart. External saddle very low down, reaching nearly as far back as the first lateral lobe. First lateral saddle and first lateral lobe broad; second lateral saddle narrow; second lateral lobe very short. Axes of these elements more or less parallel' (Van Hoepen 1965: 31).
Hluhluweoceras. 'Ammonites with suture-line consisting of a square, broad first lateral saddle, a narrower second lateral saddle and a broad but very short third lateral saddle. The external saddle is short and fairly high up. The first lateral lobe is deep and narrower than the second lateral saddle. The axes of all these elements are parallel to the keel, with the exception of the axis of the short but robust second lateral lobe which extends obliquely, more or less in the direction of the hind end of the first lateral lobe. There is only one keel which is slightly crenulated; the venter is smooth, the section square' (Van Hoepen 1965: 33).
Falsebayites. 'Ammonites with a suture-line consisting of a square, broad, first lateral saddle, a narrower but still broad first lateral lobe the sides of which are slightly convergent backwards, a short second lateral saddle and a short second lateral lobe (both these elements being narrower than the first lateral lobe); then follows a very short third lateral saddle which is as broad as high, and on the

umbilical surface are another three small lobes and saddles. The axes of all these elements are parallel to the keel. The external saddle is short and fairly low down. The whole suture is a more or less regularly meandering line. The venter is rounded; along its middle there is a broad zone which is ever so slightly raised and might be regarded as representing a keel. The ribs form a broad, very low band passing across the venter in a slightly forward direction' (Van Hoepen, 1965: 34).

Fraudatoroceras. 'Ammonites with three keels, very wide umbilicus, square section, fairly large, clavate shoulder tubercles and very long, narrow umbilical tubercles reaching up to the middle of the flanks. External saddle is half as high as the first lateral saddle which is as broad as high. First lateral lobe is very narrow. Second lateral saddle is not as broad as the first. Second lateral lobe is narrow and short. Third lateral saddle broad and short, but not as broad as the second and not reaching as far forward nor as far backwards. Third lateral lobe narrow and short not reaching as far forward or backward as the second. The umbilical seam passes through its middle. The dorsal saddle is high and narrow, higher than the first lateral saddle. There is a very small, oblique, internal lateral lobe and a small, first dorsal lateral lobe, just touching the umbilical seam. The axes of all these elements, except that of the internal lateral lobe, are parallel' (Van Hoepen 1965: 35).

According to Matsumoto's interpretation of *Peroniceras*, (Matsumoto 1965: 210) the genus is characterized by '... evolute whorls, distinctly tricarinate venter, bi-tuberculate ribs and deeply incised, particularly specialized sutures', whereas *Gauthiericeras* (Matsumoto 1965: 210) '... typically has less evolute whorls, an entire or feebly crenate ventral keel with a groove on either side, stronger ventrolateral tubercles, often double umbilical tubercles and simpler, normal collignoniceratid sutures'.

Matsumoto (1965: 210) furthermore believed that '*Peroniceras* is clearly separated from *Gauthiericeras (s. 1.)* by the different pattern of sutures and distinctly tricarinate-bisulcate venter'.

Apart from *Peroniceras* and *Gauthiericeras*, Matsumoto referred *Reginaites* and *Ciryella* to the subfamily Peroniceratinae and added four new genera: *Cobbanoceras*, type species *C. tanakai* Matsumoto, 1965; *Sornayceras*, type species *S. proteus* Matsumoto, 1965; *Ishikariceras*, type species *I. binodosum* Matsumoto, 1965; and *Reymentites*, type species *R. hataii* Matsumoto, 1965. Contrary to the opinions of both Matsumoto and Wiedmann (1978: 670), the authors prefer to place *Reymentites*, a tri- or quadrituberculate form with tricarinate venter, in the subfamily Texanitinae Collignon, 1948, rather than in the subfamily Peroniceratinae. Moreover, *Reymentites* is regarded as possibly a junior synonym of *Reginaites*, which the authors also referred to the subfamily Texanitinae (Klinger & Kennedy 1980).

Cobbanoceras is evolutely coiled with a wide umbilicus, subquadrate whorls and three entire keels on the venter, of which the middle one is higher than the lateral ones. Ribs are mostly single, and each has an umbilical and ventrolateral tubercle. The suture is rather simple.

Sornayceras has a moderate to large shell, consisting of more or less evolute whorls with wide or moderate umbilicus. The whorl section varies from subquadrate to high subrectangular with a roughly fastigiate venter. There is a distinct median keel bordered on either side by a shallow groove without distinct lateral keels. The median keel is entire or feebly crenate. The flanks are ornamented by radial ribs which are intercalated or branched, bearing umbilical and ventrolateral tubercles. The suture is deeply and finely incised and much complicated.

Ishikariceras has a shell of moderate size, evolute with wide umbilicus. The whorl section is subquadrate in early stages, but semi-elliptical in the adult. The venter is unicarinate with two shallow lateral grooves. Lateral keels, if present, are virtually indiscernible or very weak. The suture is rather simple with massive and subquadrate elements.

Etayo-Serna (1979: 97) introduced the genus *Gloriaceras*, type species *G. correai* Etayo-Serna, 1979, which has peroniceratine characteristics. The original diagnosis is as follows:

'Conchs small to moderately large. The earliest whorls observed are discoidal with fastigate, unicarinate median ventral region; the ornament consists of faint falcoid or biconcave ribs that cross the venter in an acute adoral bend; the ribs may bifurcate on the umbilical third of the flank, at this stage no tubercles are developed.

Shortly after, the ribs weaken on the median ventral line and develop a rounded somewhat spirally elongated external lateroventral node; the admedian ventral end of the ribs elongates longitudinally and which soon interconnect forming almost continuous keels on each side paralleling the median keel but the ribs can still be observed crossing the venter. The ribs sporadically develop weak peri-umbilical swellings. With growth the ribs tend to straighten on flanks, become club-like and connect the ventrolateral carinae. The periventral tubercles are much stronger than the peri-umbilical ones which sometimes are missing. The suture line has E/L saddle large, rectangular and bifid with the external branch foliate and narrow at its stem; L lobe is wide, deep, bifid (pseudotrifid), L/U2 saddle is slender, taller than E/L saddle, bifid, phylloid; U2 lobe is digitated, short. U2/U3 and U3/U1 are subequal. U3 lobe is digitated, glove-like; U1 lobe is bifid, narrower but as deep as U2; U1/I saddle is single, with a unique phylloid head.'

Another possible candidate for the subfamily Peroniceratinae is *Neogauthiericeras* Collignon, 1969, type species *N. zafimahovahi* Collignon, 1969, from the basal Campanian of Madagascar, erected for evolute forms with fastigiate venter and bituberculate ribs and suture similar to that of *Gauthiericeras*, or very close to it. Collignon did not indicate whether the genus was to be placed in the subfamily Peroniceratinae, but the name seems to imply this. The authors (Klinger & Kennedy 1980: 111) previously suggested that *Neogauthiericeras* may possibly be derived from *Reginaites* at the Santonian–Campanian stage boundary and should thus also be referred to the subfamily Texanitinae.

Patrulius & Szász (1975: 158) described a pentacarinate form of *Peroniceras* from the Coniacian of Romania. The material is fragmentary but, if more complete, would possibly be eligible for separate subgeneric or generic rank.

All these taxa, with the exception of those previously referred to the subfamily Texanitinae by Klinger & Kennedy (1980) and the enigmatic specimen from Romania are summarized in Figure 1. From the diagnoses it appears that the main characteristics for distinguishing between the various taxa are, in unweighted order:

(i) Unicarinate versus tricarinate venter,
(ii) Complex versus simple suture-line,
(iii) Evolute versus involute coiling.

The dividing lines become vague in the cases of *Fluminites, Falsebayites*, and *Sornayceras*. The validity of these various taxa and their extent is reviewed below in their proper context, as exemplified by the various species.

Genus *Peroniceras* de Grossouvre, 1894

Type species

Peroniceras moureti de Grossouvre, 1894: 100, by original designation = *Ammonites tridorsatus* Schlüter, 1867: 26.

Diagnosis

Medium-sized to large, moderately to very evolute, whorl section compressed trapezoidal to depressed quadrate. Venter with three subequal entire keels, or with the siphonal keel strongest. Ribs may be simple, prorsiradiate, straight or concave throughout, with or without umbilical bullae that migrate out to an inner flank position at maturity, or may arise in pairs or intercalate on inner whorls. All ribs develop ventrolateral tubercles. Ribs may persist to maturity, or weaken and decline on the adult body chamber.

Suture variable, from simple with short elements, as in ancestral Collignoniceratinae, or complex, with long, deeply incised elements; L more or less bifid; U_2 small and inserted below L/U.

Discussion

The diagnoses given above (pp. 130–5) by various authors indicate confusion in generic distinctions, yet *Peroniceras* is one of the most easily identified taxa if the degree of complexity of the suture is ignored. A detailed description of the type species is given below; it shares with many other species very evolute coiling, a tricarinate venter and ornament of mainly simple ribs each with an umbilical and a ventrolateral tubercle.

Its suture is relatively simple with rather broad, blocky, little-indented saddles E/L and L/U and a narrow L; U_2 and inner elements are all narrow and small. Other species, such as *P. dravidicum* Kossmat, 1895, universally referred to the genus, have much more complex, long, narrow, finely indented saddles

TAXA	COILING		VENTER		SUTURE		SUPPOSED AGE IN ORIGINAL PUBLICATIONS
	EVOLUTE	INVOLUTE	UNI-CARINATE	TRI-CARINATE	SIMPLE	COMPLEX	
Peroniceras	X			X	X	X	M. Coniacian
Gauthiericeras		X	X		X		U. Coniacian
Ciryella	X		X		X		U. Coniacian
Zuluiceras	X			X		X	M-U. Coniacian
Zuluites		X		X		X	M-U. Coniacian
Andersonites	X			X	X		U. Coniacian
Fluminites	X			X	X		U. Coniacian
Hluhluweoceras		X?	X		X		U. Coniacian
Falsebayites		X?	X		X		U. Coniacian
Fraudatoroceras	X			X	X		M. Coniacian
Cobbanoceras	X			X	X		Santonian?
Ishikariceras	X		X ------	------ ?			Coniacian
Sornayceras	X ——	—— X			X		M-U. Coniacian

Fig. 1. Summary of taxa referred to the subfamily Peroniceratinae prior to the present investigation, with identifying characteristics.

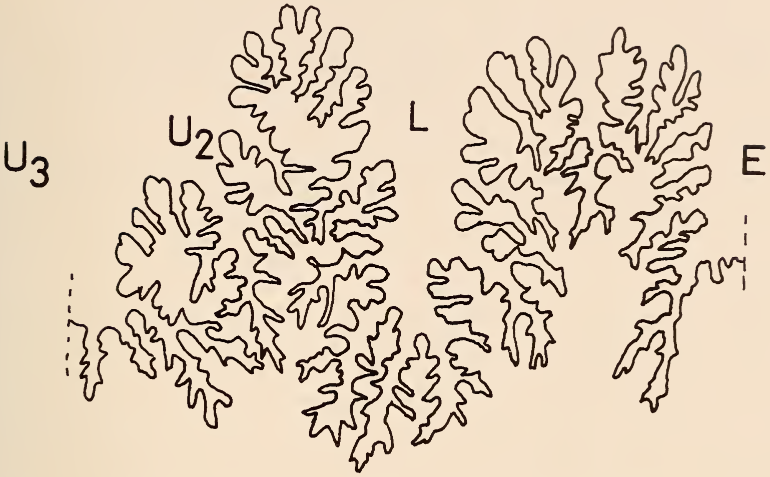

Fig. 2. External suture-line of typical *Peroniceras*, here referred to as *P. (Peroniceras) dravidicum*-type, with highly incised elements and narrow-stemmed saddles and lobes. Note the thin, stemmed saddle U_3/U_2 attached obliquely to the base of saddle L/U_2. × 1. (After Van Hoepen 1965, fig. 2a.)

with lobe U_2 distinctly inserted below saddle L/U (Fig. 2). There is great variation between species in these characters and it seems absurd to pick out particular degrees in a gradational series to typify subgenera. The simple form of suture closely resembles that of evolute species of *Subprionocyclus* Shimizu, 1926 (Collignoniceratinae) and *Protexanites* Matsumoto, 1955, and other Texanitinae except that the inner elements are narrower to accommodate the more evolute whorl. The evolutionary trend was thus from the collignoniceratine type to the *dravidicum* type.

Fraudatoroceras van Hoepen, 1965, of which *Cobbanoceras* Matsumoto, 1965, is a junior synonym, have type species with sutures that are only very slightly less developed along this line than those of *Peroniceras tridorsatum* (= *P. moureti*) and the species assigned to them, which differ in no other significant characters, should be referred to the group of *Peroniceras* centred round the type species. Indeed, *Fraudatoroceras besairiei*, the type species of Van Hoepen's genus *Fraudatoroceras*, resembles *P. tridorsatum* (= *P. moureti*) much more than do other species always referred to *Peroniceras*, both in the early stage at which tricarination sets in and in the shape of the pinched latero-umbilical bullae.

Occurrence

Middle Coniacian, world-wide. Upper Coniacian of Japan and Zululand, ?Santonian of Japan.

Subgenus *Peroniceras (Peroniceras)* de Grossouvre. 1894

(= *Fraudatoroceras* van Hoepen. 1965: 35: *Cobbanoceras* Matsumoto. 1965: 219: *Gloriaceras* Etayo-Serna. 1979: 96)

Diagnosis

Very evolute. keels strong and subequal. ribs and tubercles persist to the end of the adult body chamber.

Discussion

Observations under the discussion of the genus *Peroniceras* (p. 137) explain the basis for regarding *Fraudatoroceras* and *Cobbanoceras* as synonyms of *Peroniceras (Peroniceras)*.

The genus *Gloriaceras* Etayo-Serna. 1979 (type species *G. correaui* Etayo-Serna. 1979: 97. pl. 13 (fig. 18). pl. 14 (fig. 10). text-fig 9C–D. H) was introduced for two Colombian species that were separated from *Peroniceras* on the basis that they had an early stage with flexuous bifurcating ribs that cross the venter forming chevrons. a character retained in some adults. and also differed in suture-line. This was described as having a large. rectangular and bifid E/L saddle with the external branch foliate and narrow at its stem. L lobe wide. deep and bifid (pseudotrifid): saddle L/U_2 slender. taller than saddle E/L. bifid and phylloid: U_2 digitated and short: U_2/U_3 and U_3/U_1 subequal: U_3 digitated and glove-like: U_1 bifid. narrower but as deep as U_2: and U_1/I single with a unique phylloid head. This was contrasted with the suture of *P. moureti* on the basis of de Grossouvre's figure. which he described as having a wide E/L. with narrow. highly incised digitated L. U_2/U_3 accessory to L/U_2. and a similar interdependency of L/U_2–U_2/U_3 was noted in *P. dravidicum* on the basis of Kossmat's figure (1895. pl. 23 (fig. 3)).

Juvenile *Peroniceras (Peroniceras)* of several species have. at 10–15 mm diameter. a strong. entire or undulose siphonal keel flanked by shallow grooves and weak lateral keels. which may also be undulose. strengthening at the termination of the ribs. This stage is rapidly replaced by a distinctly tricarinate one in which undulations are either lost or are irregular and correspond to the ribs. *Gloriaceras correaui* differs only in the more obvious development of this feature and the retention of rather more marked undulations of the lateral keels. in these respects retaining the phylogenetically primitive features of the ancestral Collignoniceratinae a little longer than some other specimens. Etayo-Serna also noted that the ribs extend to the siphonal keel in *Gloriaceras*. This is no more so than in some specimens of the type species of *Peroniceras (Peroniceras)*: the juvenile SAS Z734. illustrated as Figure 16D–E (the original of Van Hoepen 1965. pl. 2). in fact shows all the supposedly diagnostic features of *Gloriaceras*. which is here treated as a strict synonym.

Zuluiceras van Hoepen. 1965. of which *Zuluites* van Hoepen. 1965. and *Sornayceras* Matsumoto. 1965. are regarded as synonyms. is discussed fully below (p. 180). They represent a series of progressively more involute forms, the earliest of which, *Zuluiceras aberlei* (Redtenbacher, 1873) and *Z. bajuvaricum* (Redtenbacher, 1873) occur with *Peroniceras* (*Peroniceras*). These early forms (*Zuluiceras* s.s.) are linked by a continuum to much more involute later forms ('*Zuluites*'), the series showing progressive decline in ornament. The earliest species are close to *Peroniceras* (*Peroniceras*) and *Zuluites* is in consequence afforded subgeneric status only. The two differ in the greater involution of *Zuluiceras*, the compressed whorls that tend to round, lateral keels that are weaker than the siphonal one, and adults that retain only weak ornament or none.

Peroniceras (*Peroniceras*) is easily distinguished from *Gauthiericeras* de Grossouvre, 1894, which has a strong, sometimes serrated siphonal keel flanked by grooves and only incipient lateral keels, and strong primary ribs that may branch at umbilical or lateral tubercles.

Ishikariceras Matsumoto, 1965, has inner whorls with a subquadrate section, coarse bituberculate ribs and a strong siphonal keel but no, or only very weak, side keels, the body chamber being oval and virtually smooth with only constrictions and a single keel.

Reginaites Reyment, 1957, of the Texanitinae, of which *Reymentites* Matsumoto, 1965, is a synonym (Klinger & Kennedy 1980), is tricarinate with umbilical and ventrolateral tubercles only on nuclei, the ventrolateral splitting in two at a later stage when feeble lateral tubercles may appear.

Occurrence

Middle Coniacian, world-wide. *P.* (*Peroniceras*) ['*Cobbanoceras*'] *tanakai* Matsumoto, 1965, is questionably dated as approximately Santonian (Matsumoto 1965: 220).

Peroniceras (*Peroniceras*) *tridorsatum* (Schlüter, 1867)

Figs 3–15, 16D–E

Ammonites tridorsatus Schlüter, 1867: 26, pl. 5 (fig. 1).
Ammonites cf. *tridorsatus* Schlüter, 1876: 158, pl. 41 (figs 3–5).
? *Ammonites* (*Schloenbachia*) *czörnigi* Redt: Fallot, 1885: 229, pl. 1 (fig. 1).
Peroniceras subtricarinatum var. *tridorsatum* Schlüter: de Grossouvre, 1894: 96, pl. 10 (figs 2–3), pl. 11 (fig. 1).
Peroniceras moureti de Grossouvre, 1894: 100, pl. 11 (figs 3–4), text-figs 37, 39; Pruvost, 1910: 367; Stolley, 1916: 89; Diener, 1925: 150; Venzo, 1936: 101, pl. 9 (fig. 1); Young, 1963: 73, pl. 26 (fig. 5), pl. 27 (fig. 1), text-fig. 13(a); ?Collignon 1965: 60, pl. 440 (fig. 1807); Szász & Lăcătuşu, 1974: 209, pl. 6 (fig. 3), pl. 7 (fig. 3); Wiedmann, 1978: 669, pl. 2 (figs 4–5); Amedro & Robaszynski, 1978: 37, pl. 1 (fig. 2); Collignon *et al.* 1979: 392, pl. 2 (fig. 3); Szász, 1981: 106, pl. 9 (figs 3–4).
Peroniceras (*Peroniceras*) *besairiei* van Hoepen, 1965: 4, pl. 1, text-fig. 1a.
Fraudatoroceras besairiei van Hoepen, 1965: 36, pl. 27, text-fig. 9a–b.
Peroniceras besairiei van Hoepen: Collignon, 1965: 54, pl. 437 (fig. 1803), pl. 438 (fig. 1803).
Peroniceras rousseauxi de Grossouvre, 1894: 102, pl. 11 (fig. 5); Diener, 1925: 151.
Peroniceras cf. *moureti* de Grossouvre: Maury, 1907: 87; Diener, 1925: 151.

Peroniceras tridorsatum (Schlüter): Stolley, 1916: 89. Diener, 1925: 152. Van Hoepen, 1965: 7, pl. 2. Amedro & Robaszynski, 1978: 36, pl. 2 (fig. 1), pl. 3 (figs 1–2). Szász, 1981: 107, pl. 9 (fig. 2).
? *Peroniceras tricarinatum* d'Orbigny: Scupin, 1913: 93, pl. 3 (fig. 5).
Peroniceras l'epeei (Fallot): Mirăuţă & Mirăuţă 1964: 336, pl. 7 (fig. 2), pl. 11. ?Joja & Chiriac, 1964: 46, pl. 1 (fig. 5).
? *Peroniceras* cf. *tridorsatum* (Schlüter): Collignon, 1965: 58, pl. 439 (fig. 1805, *non* 1806).
? *Peroniceras* aff. *tridorsatum* (Schlüter, 1867): Amedro & Robaszynski, 1978: 37, pl. 2 (fig. 2).
Peroniceras sp. (aff. *Peroniceras rousseauxi* Grossouvre): Szász & Lăcătuşu, 1974: pl. 2 (fig. 4), pl. 7 (fig. 4).
Peroniceras (Peroniceras) tridorsatum (Schlüter, 1867): Kennedy, in press.

Type specimens

The holotype of the species, from the Coniacian of Westphalia, is lost. The holotype, by original designation, of *Peroniceras moureti* de Grossouvre, 1894, is the original of De Grossouvre's pl. 11 (fig. 4) from the 'Calcaires tendres gréseaux de la base de la Craie de Villedieu. Courtiras, près Vendôme (Loir-et-Cher)'. It is in the collections of the École des Mines, now in the Université Claude Bernard, Lyon. Paratypes include the specimen figured by De Grossouvre as his pl. 11 (fig. 3), an unregistered specimen in the collections of the Sorbonne (now in the Université Pierre et Marie Curie, Paris) from Assize L^1 of Arnaud at La Boulenerie, near Jonzac (Charente-Maritime) and a specimen (ML 7) from the Coniacian of Lezennes (Nord) in the Musée Gosselet, Lille.

The holotype, by monotypy, of *Peroniceras rousseauxi* de Grossouvre, 1894, is an unregistered specimen in the collections of the Sorbonne from Assize L^1 of Arnaud at St. Simon-de-Jonzac (Charente-Maritime).

The holotype, by original designation, of *Peroniceras (Peroniceras) besairiei* van Hoepen, 1965, is SAS Z248.

The holotype, by original designation, of *Fraudautoroceras besairiei* van Hoepen, 1965, is SAS Z756.

Material

SAS Z1117, SAS A63, and NMB D1145a–e, all from locality 72, degraded river cliff on the north side of the Mzinene River downstream from the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1590 and Z1522 from locality 91, degraded river cliff and artificial cut near the Hluhluwe River estuary, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, undifferentiated Coniacian debris. SAS Z1623a–b, Z1607, and SAM–PCZ5942 from locality 92, bulldozer scrapings and adjacent hillslopes on the farm Panplaas east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z248, Z730 and Z1120 from locality 73, degraded river cliffs on the north bank of the Mzinene River downstream of the Munywana River junction, Zululand, St. Lucia Formation, Coniacian II and III.

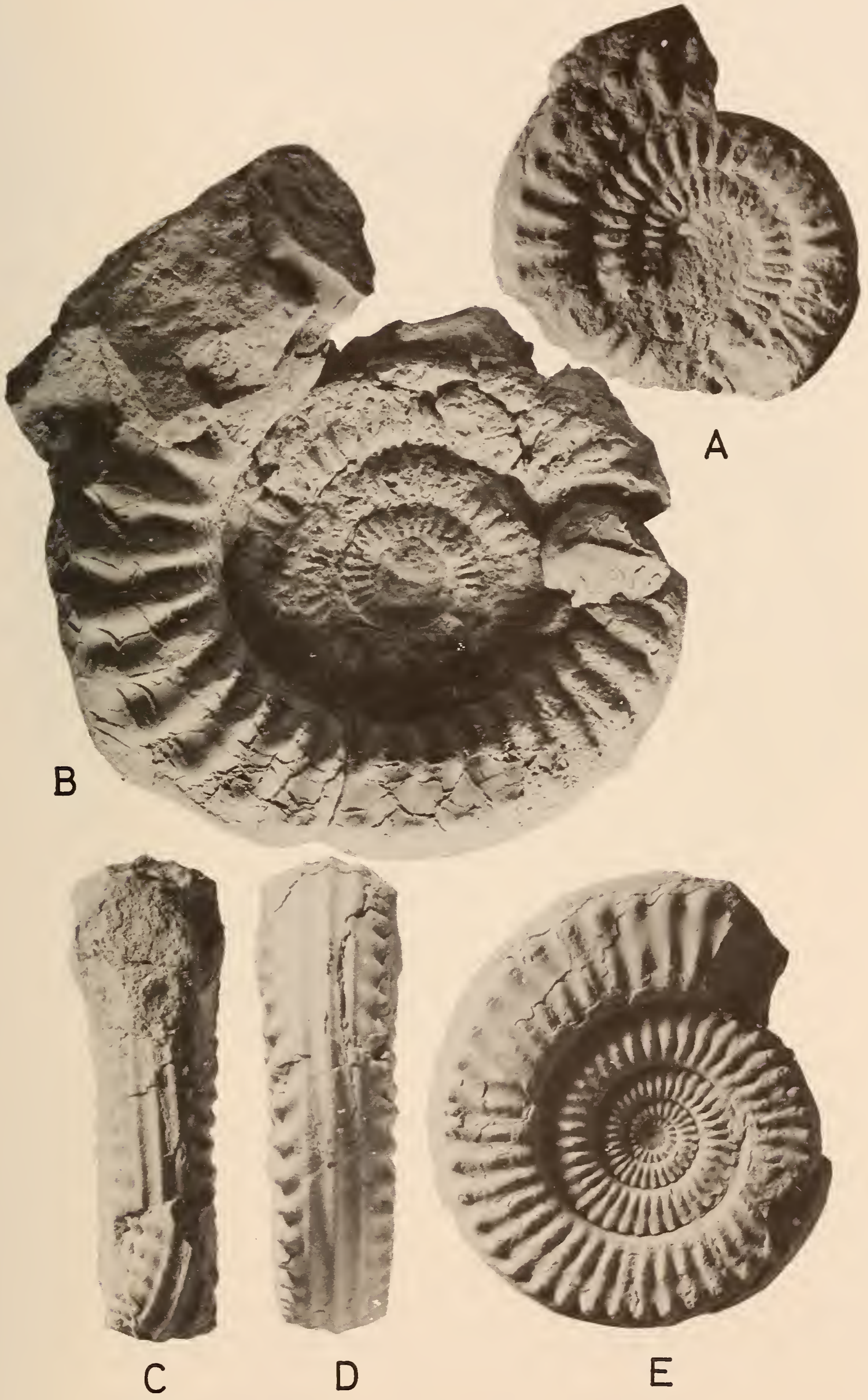

Fig. 3. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). A. SAS A63. B. NMB–D1145a. C–E. SAS Z1117. All × 1.

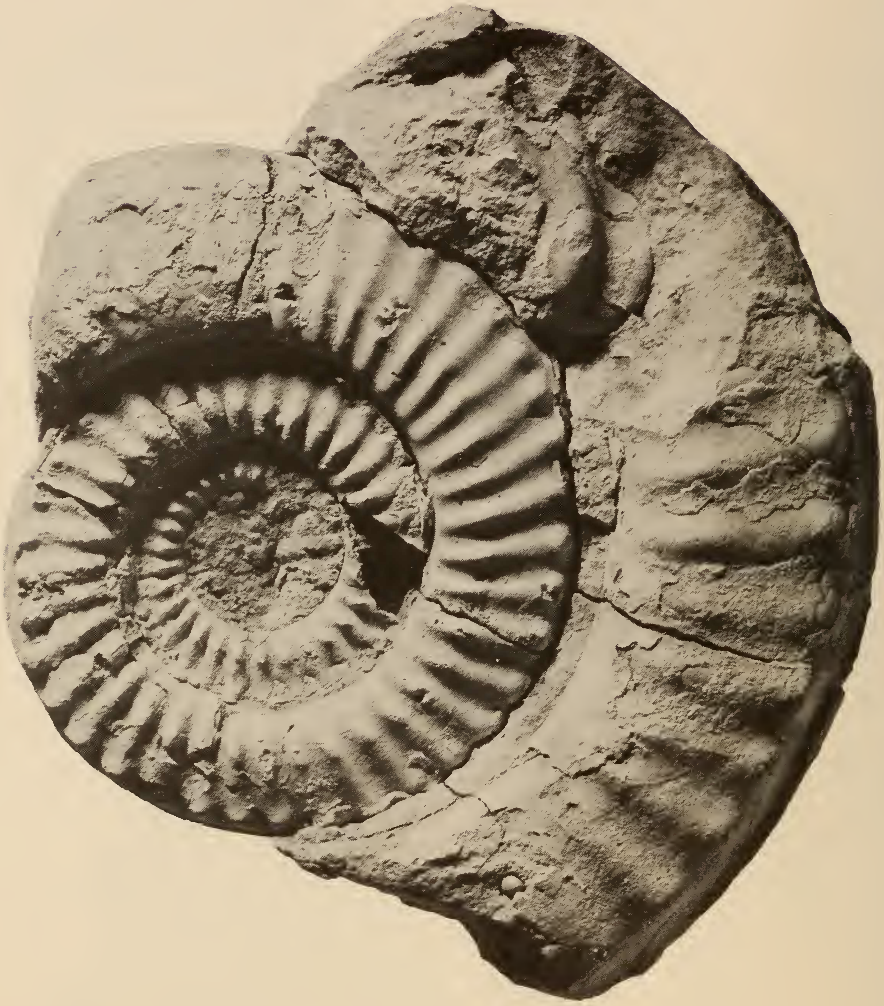

Fig. 4. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). NMB D1145e. Specimen with distinct latero-umbilical tubercles on inner whorls, but indistinct on outer whorls, as in *P. (P.) lepeei* (Fallot, 1885). × 1.

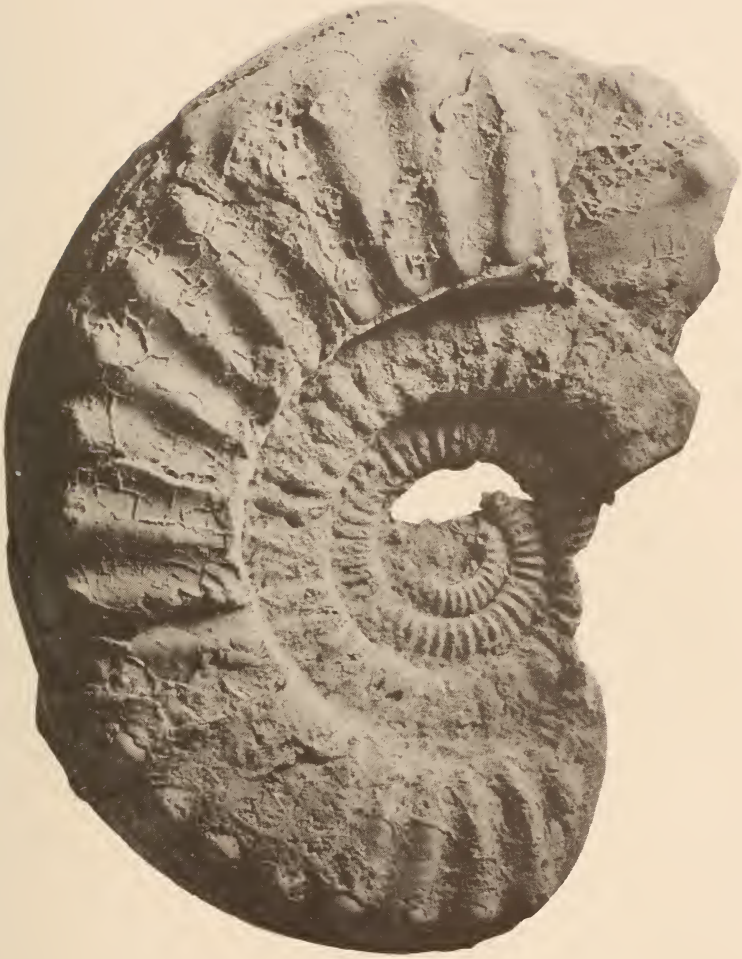

Fig. 5. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). NMB D1145C. Specimen with narrower umbilical width than usual. × 1

Dimensions

	D	*Wb*	*Wh*	*Wb*/*Wh*	*U*	*R*
D1145a	31,0	9,0(29,0)	9,0(29,0)	1,0	16,0(51,6)	32:34
Z1623b	42,7	13,2(30,9)	12,5(29,2)	1,05	20,5(48,0)	28:28
Z1623a	52,4	17,0(32,4)	12,5(23,8)	1,36	27,0(52,0)	26:26
Z1117	59,0	17,0(28,8)	17,0(28,8)	1,0	31,0(52,5)	38:38
Z1607	60,0	17,0(28,0)	17,7(29,5)	1,04	29,1(48,5)	30:30
Z1120	63,3	19,0(30,0)	19,6(30,9)	0,96	30,5(48,0)	21:21
Z1590	82,8	24,6(29,7)	22,0(26,5)	0,92	48,0(57,9)	28:28
Z730	101,6	25,6(25,1)	23,3(22,9)	1,09	60,0(59,0)	30:30
Z1522	112,0	30,0(26,7)	26,0(23,2)	1,15	65,0(58,0)	24:24
D1145c	119,0	—	40,0(33,6)	—	55,0(46,2)	—
Z756	120,0	33,7(28,0)	27,3(22,7)	1,23	71,0(59,0)	33:33
D1145e	124,0	36,0(29,0)	34,0(27,4)	1,05	66,0(53,2)	38:38
Z248	132,0	33,0(25,0)	33,0(25,0)	1,0	73,0(53,0)	29:29

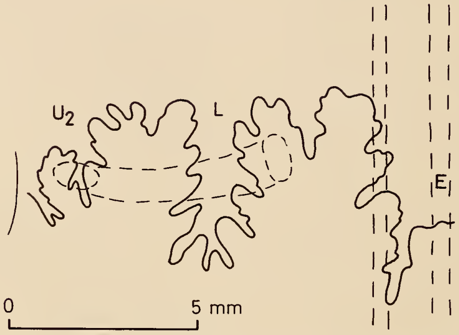

Fig. 6. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). External suture of SAS A63.

Description

Coiling is very evolute, with an umbilical width of the order of 48 to 59 per cent of the diameter, and with the whorls overlapping only slightly.

The whorl section is rounded to subrectangular, varying from compressed to depressed, with the greatest costal width at the umbilical tubercle.

There is an initial smooth stage, which may persist to a diameter of 9 mm; thereafter umbilical tubercles connecting to ventrolateral tubercles via weak ribs appear. With increasing diameter all ornament becomes stronger, with prominent umbilical bullae situated well away from the umbilical edge on the flanks and connected to rounded or slightly clavate ventrolateral tubercles by prominent ribs. The ribs are generally single but occasional bifurcations occur, especially on the inner whorls. All ribs are slightly prorsiradiate and curved. Strong spiral ridges are commonly developed.

The venter is prominently tricarinate, with the central keel strongest. The suture is relatively simple but variable with blocky elements (Figs 12–13).

Discussion

Kennedy (in press) has discussed the difficulties in interpreting Schlüter's lithograph of the lost holotype, and concluded that the variable, closely and simply ribbed *Peroniceras (P.)* with persistent umbilical–umbilicolateral bullae that

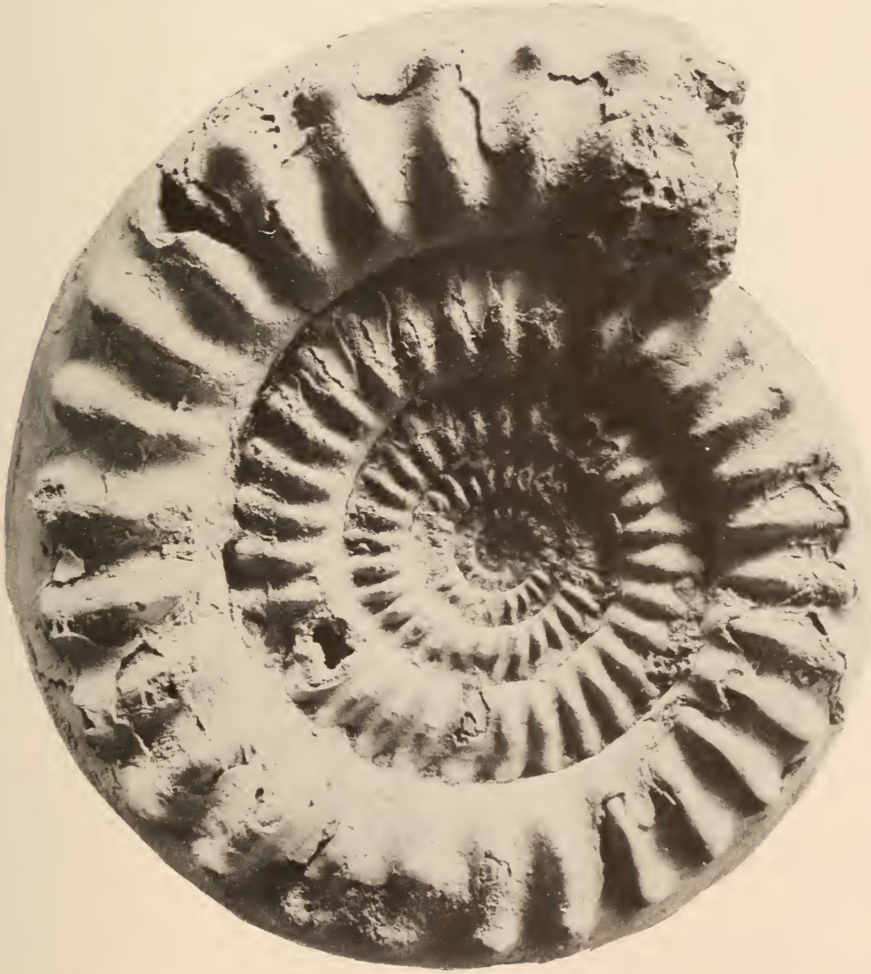

Fig. 7. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z248, the holotype of *P. (Peroniceras) besairiei* van Hoepen, 1965. × 1.

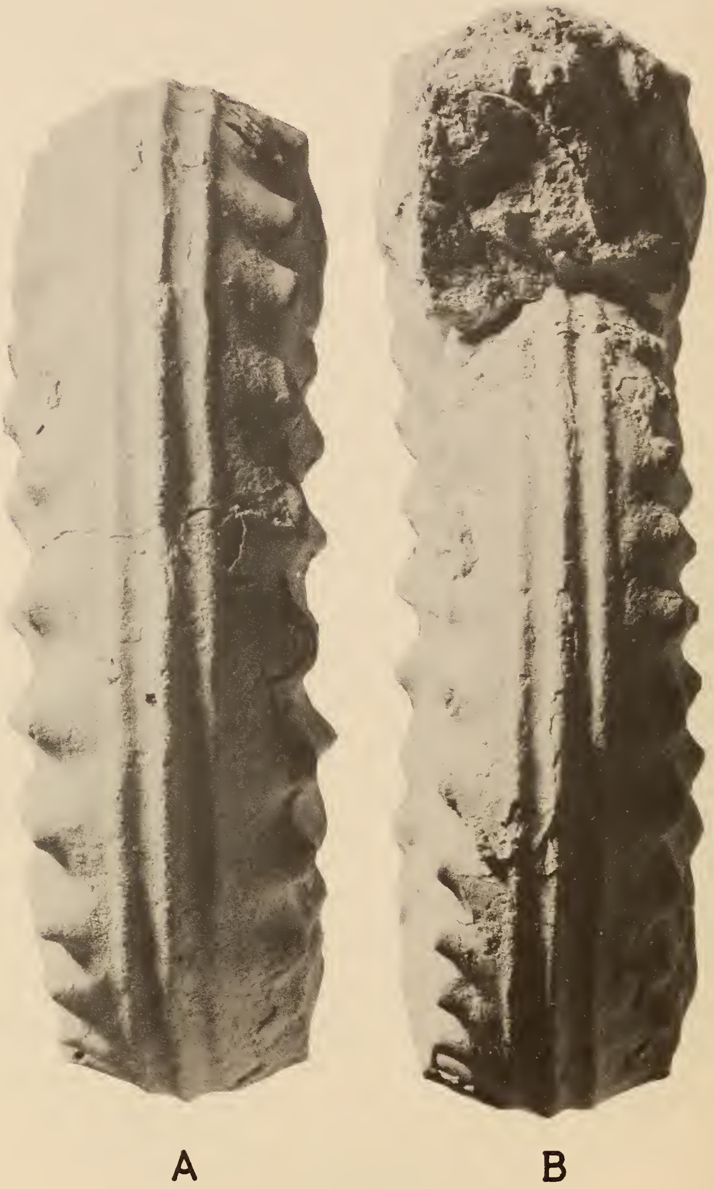

Fig. 8. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z248 the holotype of *P. (Peroniceras) besairiei* van Hoepen, 1965. × 1.

occur in France and Germany (*P. tridorsatum, moureti*, and *rousseauxi*) represent but a single species, a view followed here.

P. (P.) lepeei (Fallot, 1885) differs from the present species in having delicate dense ribs that lack umbilical bullae; it is discussed further below. There are, however, transition forms such as NMB D1145e (Fig. 4) that have a more angular whorl section and weakening ornament on the outer whorl.

P. (P.) besairiei van Hoepen, 1965, is based on a depressed variant of this species that is close to the holotype of De Grossouvre's *P. (P.) rousseauxi*, also regarded as a synonym. Van Hoepen was misled in his interpretation of *P. (P.) besairiei* by the illustrations of Besairie (1930, pl. 64 (figs 4–6)) and Venzo (1936,

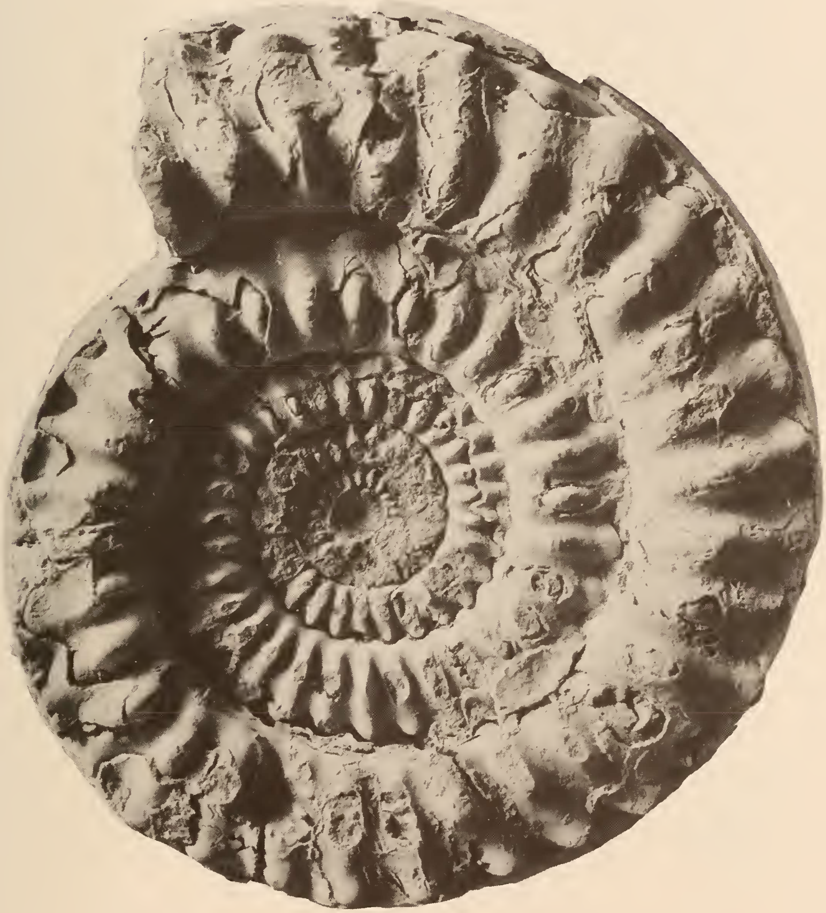

Fig. 9. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z786, the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. × 1.

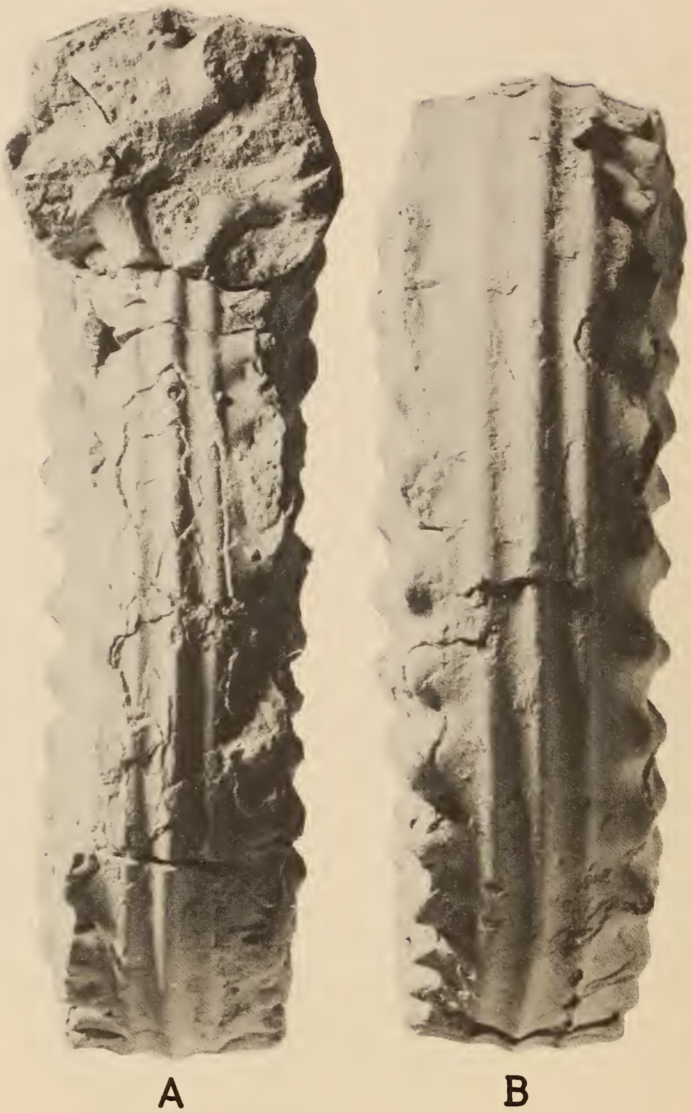

Fig. 10. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z786, the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. × 1,2.

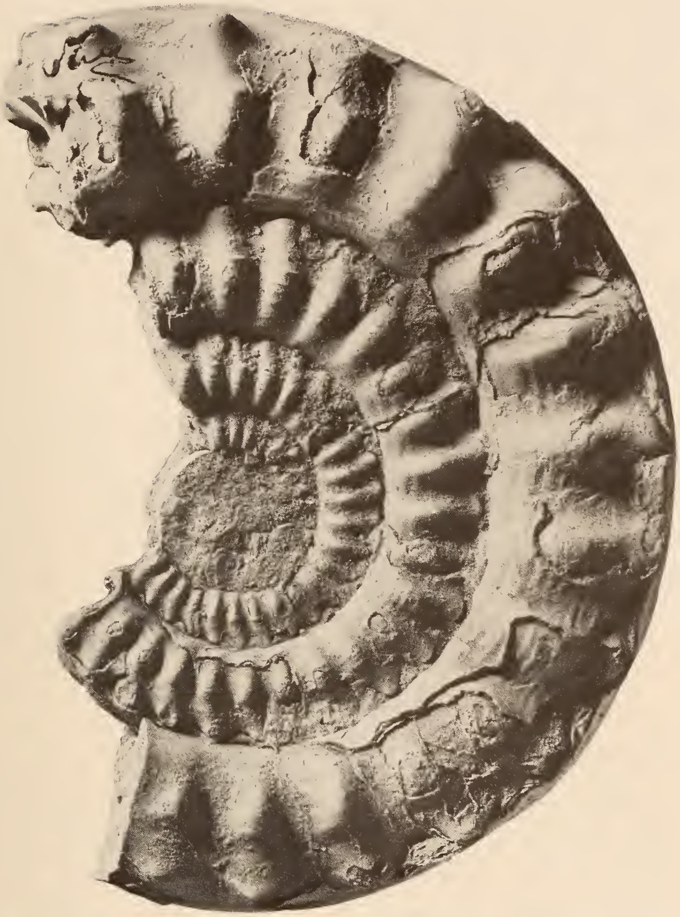

Fig. 11. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z1522, with stronger lateral ornament than the other specimens, and distinct spiral ornament. × 1.

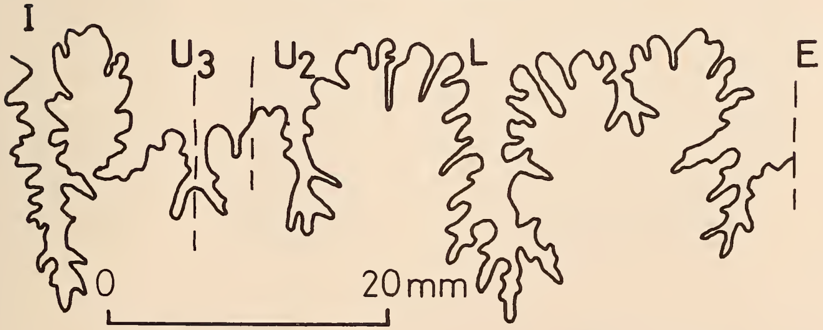

Fig. 12. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). Complete suture-line of SAS Z786.

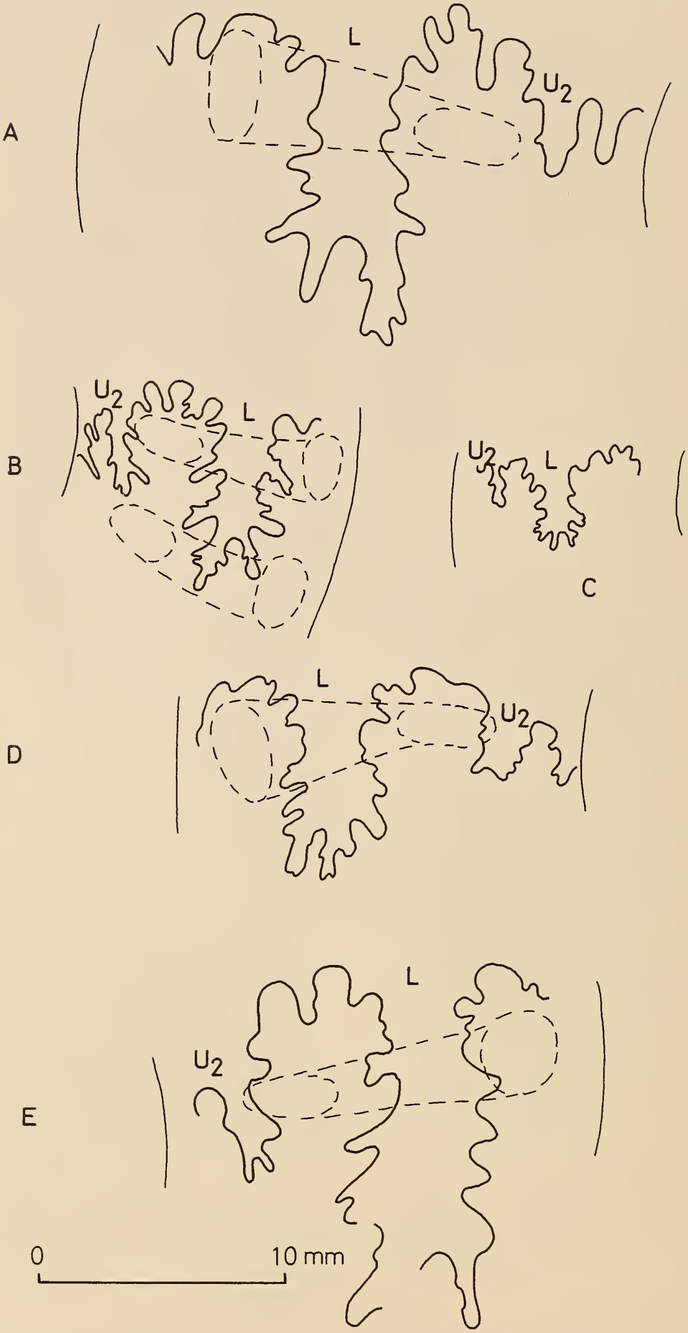

Fig. 13. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). Suture-lines of different specimens. A. SAS Z248, part of the suture-line of the holotype of Van Hoepen's *Peroniceras (Peroniceras) besairiei*, alleged to be of the *P. (P.) dravidicum* type. B–C. SAS Z1623. D. SAM–PCZ5942. E. SAS Z730.

pl. 11 (fig. 9)). According to Van Hoepen (1965: 36), *P. (P.) besairiei* and his *Fraudatoroceras besairiei* are 'practically the same in shape and ornamentation. . . . The only difference is the suture-line'. He believed that *F. besairiei* had a simple block-type suture-line, whereas *P. (P.) besairiei* (interpreted according to Besairie's figures) was alleged to have a complex *Peroniceras* (*dravidicum*)-like suture-line. Examination of the holotype of *P. (P.) besairiei* shows that the suture-line (which according to Van Hoepen could not be developed) is of the same type as that of *F. besairiei* (Figs 12–13). They are synonyms, homonyms when in the same genus, and both synonyms of *P. (P.) tridorsatum*. Van Hoepen also erred in regarding his *P. (P.) besairiei* as the same as Besairie's (1930: 634, pl. 46 (figs 4–6)) *Peroniceras subtricarinatum* and Venzo's (1936: 99, pl. 10 (fig. 1) pl. 11 (fig. 9)) *Peroniceras dravidicum*, and he assumed that the suture-lines would be identical. The specimens described by Besairie may partially include *P. (P.) tridorsatum* as some specimens were said to have single ribbing, but the figured specimens definitely do not belong to *P. (P.) tridorsatum* as the complex suture-line and bifurcating ribbing shows. The specimen figured by Venzo probably belongs to *P. (P.) dravidicum*. Collignon (1965: 54, pl. 437 (fig. 1803), pl. 438 (fig. 1803)) described and figured a specimen under the name of *Peroniceras besairiei*, but unfortunately did not describe the suture-line; neither is it visible in the figures.

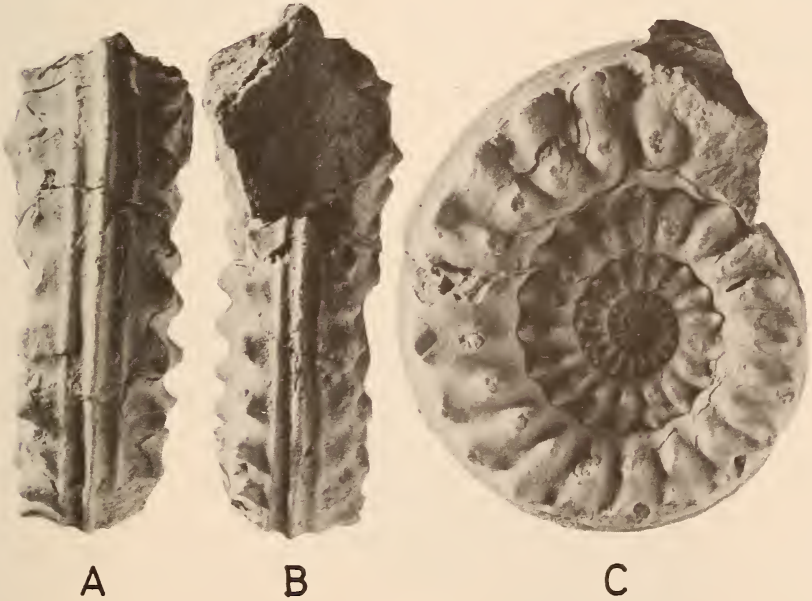

Fig. 14. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). A–C. SAS Z1120.× 1.

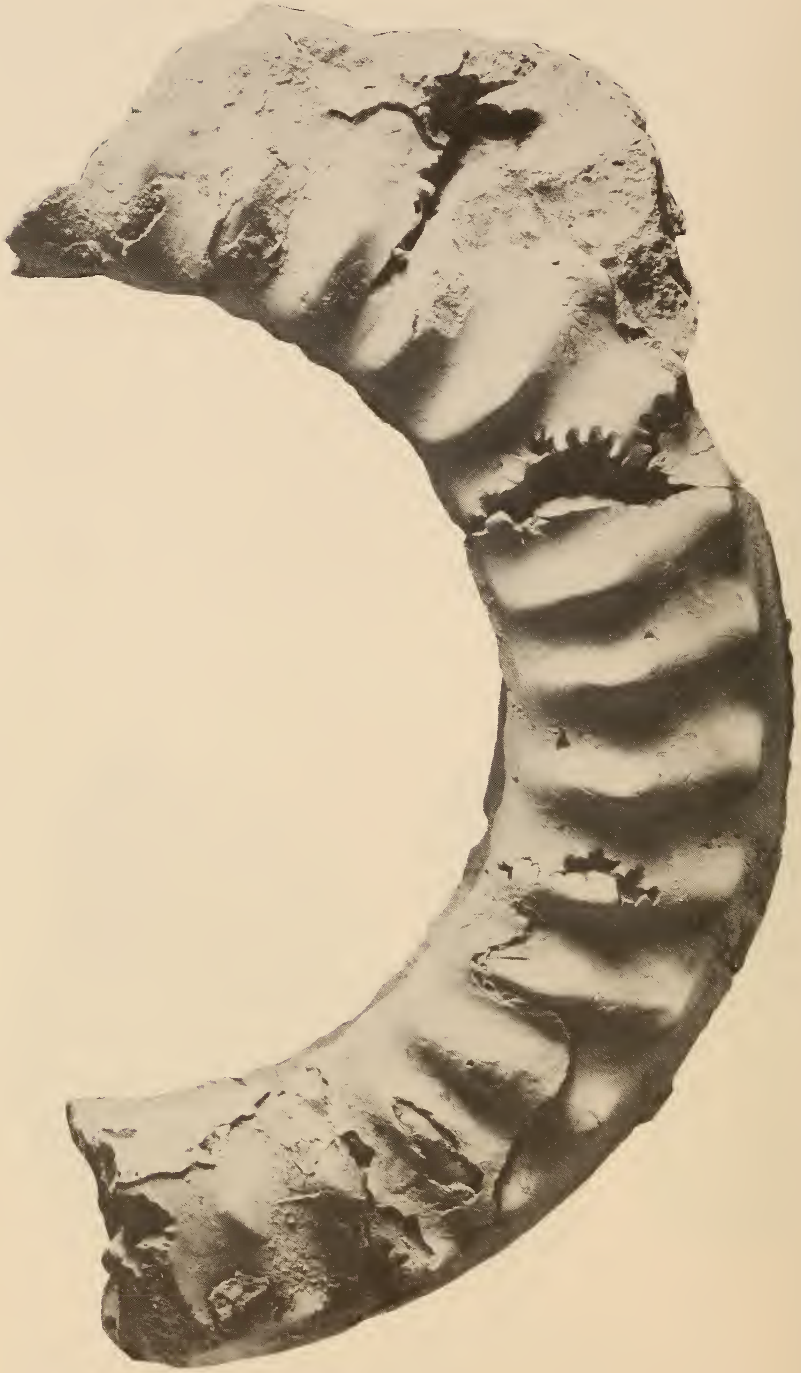

Fig. 15. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z756, the outer phragmocone whorl of the holotype of *Fraudatoroceras besairiei* van Hoepen, 1965. × 1. (See also Figs 9–10.)

Specimens the authors refer to *Peroniceras (P.) subtricarinatum* may resemble *P. (P.) tridorsatum* superficially, but differ in having occasionally bifurcating ribs and a more complex, incised suture-line.

P. (P.) ninakawai (Matsumoto 1965: 223, pl. 37 (fig. 2), text-figs 7–8) from the 'Santonian' of Hokkaido has a narrower umbilicus (41–42 %) than many *P. (P.) tridorsatum* specimens (48–49 %) and develops strong, widely spaced auricular ribs on the outer whorls.

Occurrence

Middle Coniacian *P. (P.) tridorsatum* Zone of western, central and southern Europe, Gulf coast of the United States, Coniacian II and III of Zululand.

Peroniceras (Peroniceras) lepeei (Fallot, 1885)

Figs 16A–C, 17–18

Ammonites (Schloenbachia) L'Epeei Fallot, 1885: 231, pl. 1 (fig. 2.).
Peroniceras L'Epeei (Fallot): Desio, 1920: 208, pl. 12, (figs 6–7), pl. 14 (fig. 6). Diener, 1925: 150. Kennedy, in press.

Type specimen

The holotype, by monotypy, is the original of Fallot (1885 pl. 1 (fig. 2)), from the Grès Verts de Dieulefit of Dieulefit, Drôme, south-eastern France, Middle Coniacian, *Peroniceras (P.) tridorsatum* Zone. The specimen is preserved in the collections of the Laboratoire de Géologie of the Faculté des Sciences, Grenoble.

Material

SAS Z1568 from locality 92, bulldozer scrapings and adjacent hillslopes on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II or III. SAS A1989 from locality 72, degraded river cliff on the north side of the Mzinene River downstream from the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II or III.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
Z1568	52,0	15,5(29,8)	14,2(27,3)	1,09	27,7(53,2)

Description

Coiling is polygyral, very evolute with an umbilical diameter of 53 per cent. The whorl section is variable, both between specimens and at different stages of ontogeny (Fig. 18A). It is initially ovoid and compressed, but thereafter rectangular with flattened flanks.

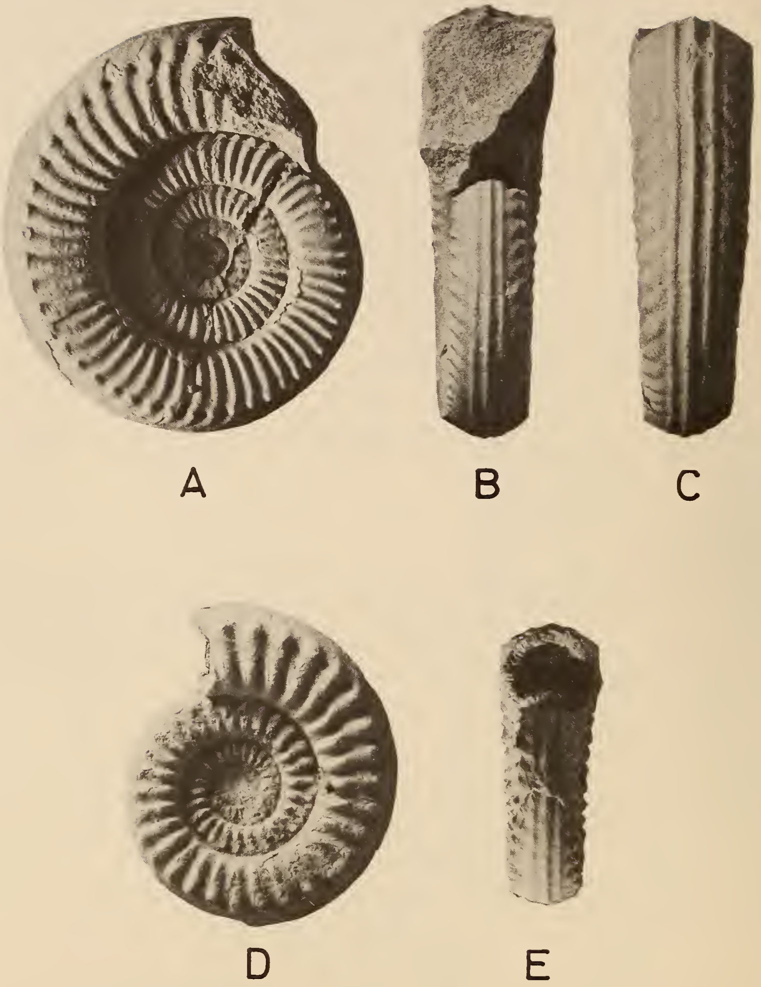

Fig. 16. A–C *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). SAS Z1568. D–E. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). SAS Z734. All × 1.

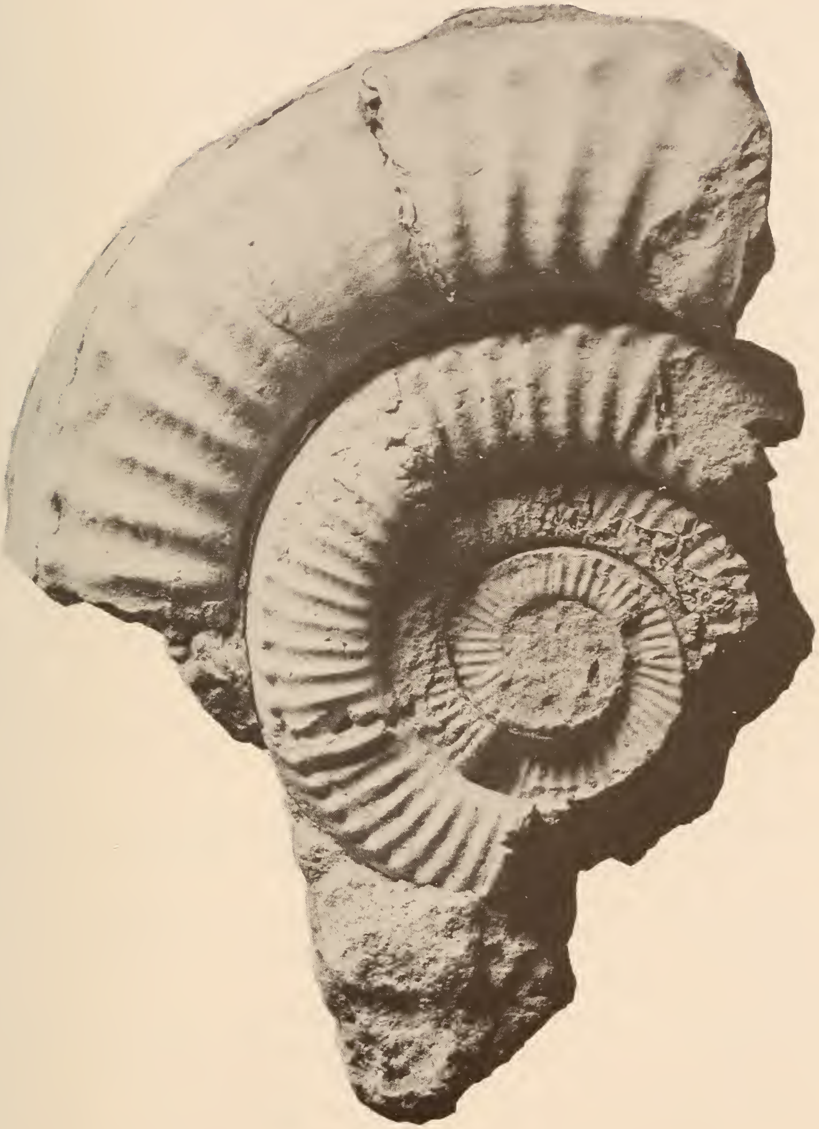

Fig. 17. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). Large specimen showing the relatively simple suture-line and faint spiral ornament on the body chamber. SAS A1989. × 1.

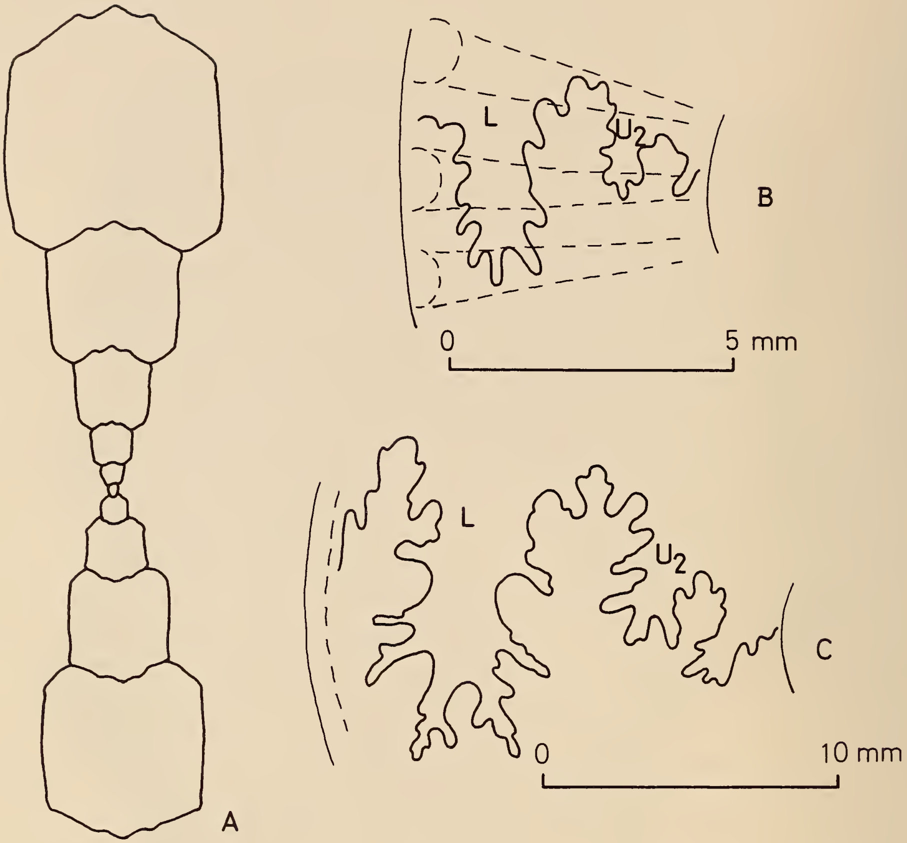

Fig. 18. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). A. Whorl section of SAS Z1568. × 1,5. B. External suture of SAS Z1568. C. External suture of SAS A1989.

It remains so in SAS Z1568 (Fig. 16A–C), but reverts to being rounded in SAS A1989 over the greater part of the phragmocone and body chamber, with no clearly defined umbilical edge (Fig. 17).

On the innermost whorls of SAS Z1568 the flanks are completely smooth up to a diameter of 6 mm, and the venter is fastigiate with a feeble siphonal ridge. Beyond that diameter tubercles appear in the umbilical seam of the succeeding whorl, and at a diameter of 18 mm adult ornament is fully developed. This consists of delicate, concave, prorsiradiate ribs each bearing a clavate tubercle. There are 50 ribs per whorl in SAS Z1568 (Fig. 16 A–C). Ribbing is generally simple but occasional bifurcations occur in SAS A1989 (Fig. 17). Parts of the body chamber of both specimens show delicate spiral ornament. The venter is tricarinate, with the median keel strongest. The suture is rather simple, with massive saddles and lobes (Fig. 18 B–C).

Discussion

This is a very poorly known species, thus far described only from the Middle Coniacian of France and Italy. The species is characterized by the delicate, concave prorsiradiate ribs, absence of umbilical tubercles, and flattened flanks.

It is very close to *P. (P.) tridorsatum* (= *P. (P.) moureti*), and the two occur together. De Grossouvre (1894: 101) had already pointed to the similarities between the species, and Desio (1920: 208) even included *P. (P.) moureti* in the synonomy of *P. (P.) lepeei*. The only difference is the absence of umbilical tubercles in *P. (P.) lepeei*. The specimen figured by Schlüter (1876, pl. 4 (figs 3–5)) as *Ammonites* cf. *tridorsatus*, and included in the synonomy of *P. (P.) moureti* by De Grossouvre, has umbilical tubercles on the inner whorls but these become progressively weaker on the outer whorl. Similar though more coarsely ornamented specimens of *P. (P.) tridorsatum* also occur in Zululand and this suggests a close relationship between the two species.

The suture-lines of the two species are similar, having relatively simple blocky elements but lack the narrow-stemmed elements typical of the *P. (P.) dravidicum*-type suture.

Occurrence

Middle Coniacian, *P. (P.) tridorsatum* Zone of Dieulefit (Drôme), Coniacian (precise horizon unknown) of Touraine (condensed Calcaires durs de la Ribochère) in France, Italy, and Coniacian II or III of Zululand.

Peroniceras (Peroniceras) subtricarinatum (d'Orbigny, 1850)

Figs 19A–B, D–E, 20–23

Ammonites tricarinatus d'Orbigny, 1841: 307, pl. 91 (figs 1–2). Schlüter, 1872: 44, pl. 13 (figs 1–4). Fritsch 1872: 26, pl. 1 (figs 1, 3, *non* 2).

Ammonites subtricarinatus d'Orbigny, 1850: 212. ? Ooster, 1858: 151, pl. 26 (figs 10–11). Drescher, 1863: 331, pl. 8 (figs 2, 4). *Non* Stoliczka, 1865: 54, pl. 31 (fig. 3).

Ammonites (Schloenbachia) subtricarinatus d'Orbigny: Fritsch, 1889: 70; 1893: 74; 1897: 36.

Peroniceras subtricarinatum d'Orbigny: de Grossouvre, 1894: 94 (pars), pl. 10 (fig. 1, *non* 2–3), *non* pl. 11 (figs 1–2). *Non* Sturm, 1900: 60, pl. 3 (fig. 5). Pervinquière, 1907: 249. Pruvost, 1910: 365. Stolley, 1916: 89. Burckhardt, 1921: 112, pl. 29 (figs 5–6 only). Diener, 1925: 151. Besairie, 1930: 634, pl. 66 (figs 4–6), text-fig. 2.1. Andert, 1934: 406. Collignon, 1965: 58, pl. 439 (fig. 1804). Thomel. 1969: 119, pl. F (figs 1–2). Amedro & Robaszynski, 1978: 35, pl. 1 (fig. 3). Collignon *et al.* 1979: 390, pl. 1 (fig. 1).

Schloenbachia (Peroniceras) subtricarinatum d'Orbigny: Boule, Lemoine & Thévenin, 1907: 22.

Peroniceras aff. *tricarinatum* d'Orbigny: Böse, 1928: 268, pl. 11 (figs 2–4).

Peroniceras tenuis van Hoepen, 1965: 7, pl. 3, text-fig. 1b–e.

Peroniceras tenue van Hoepen: Collignon, 1965: 66, pl. 443 (fig. 1814).

Peroniceras (Peroniceras) subtricarinatum (d'Orbigny, 1850): Kennedy, in press.

Type specimens

D'Orbigny (1841: 308) referred two specimens to his *Ammonites tricarinatus*, which he subsequently (1850: 212) renamed *Ammonites subtricarinatus* be-

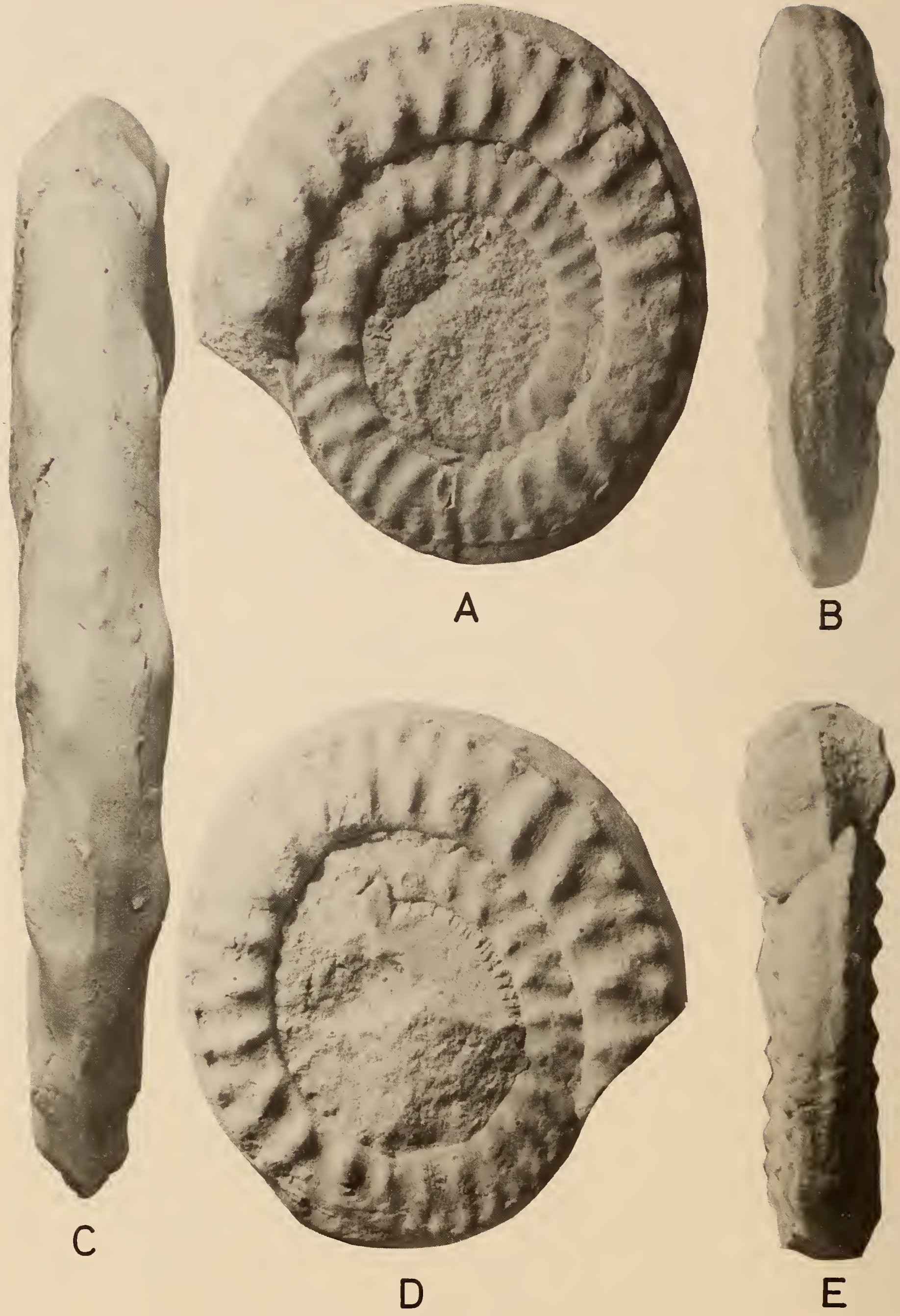

Fig. 19. A–B, D–E. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). The lectotype from the Lower Coniacian near Rennes-les-Bains, France. × 1. C. *Gauthiericeras margae* (Schlüter, 1867), holotype. × 0,6. (See Figs 94–95 for details.)

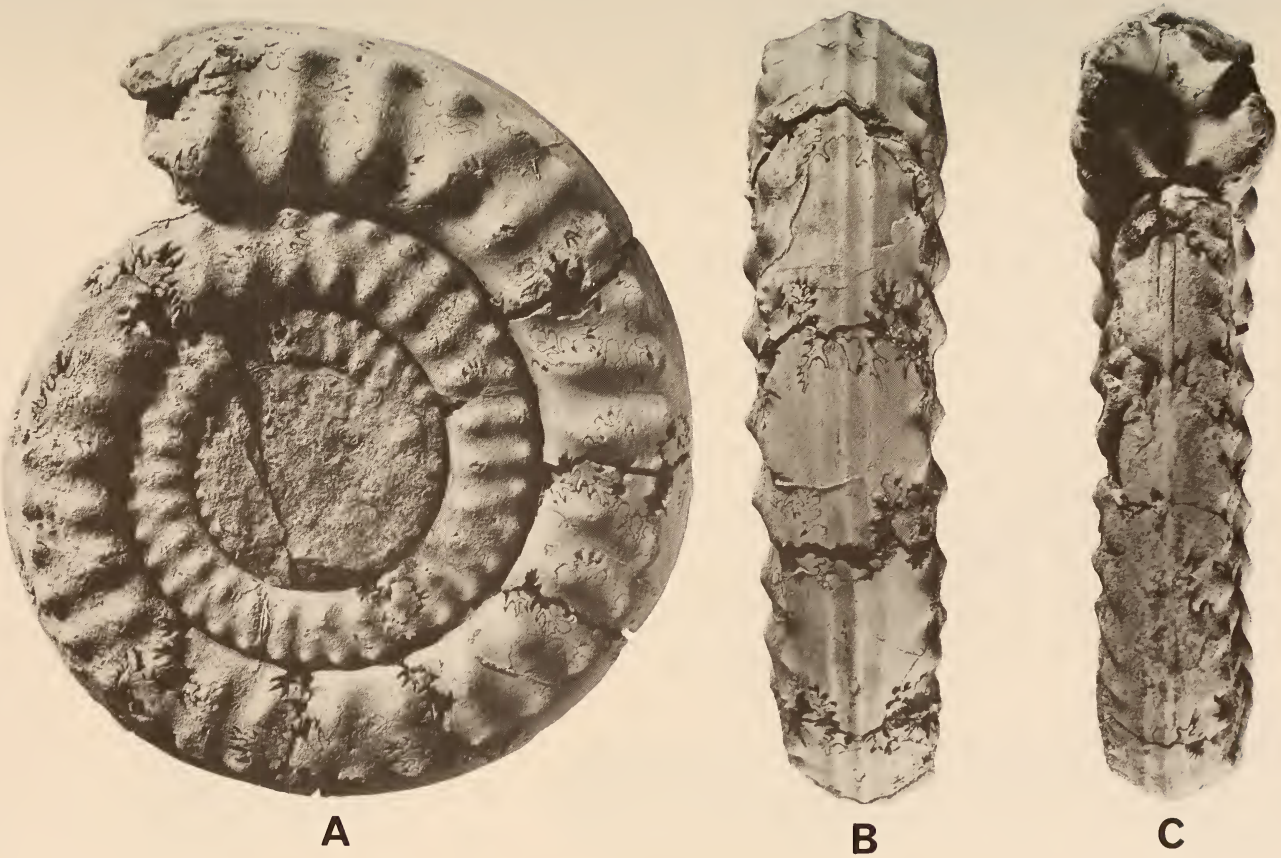

Fig. 20. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). SAS Z1002. × 0,67.

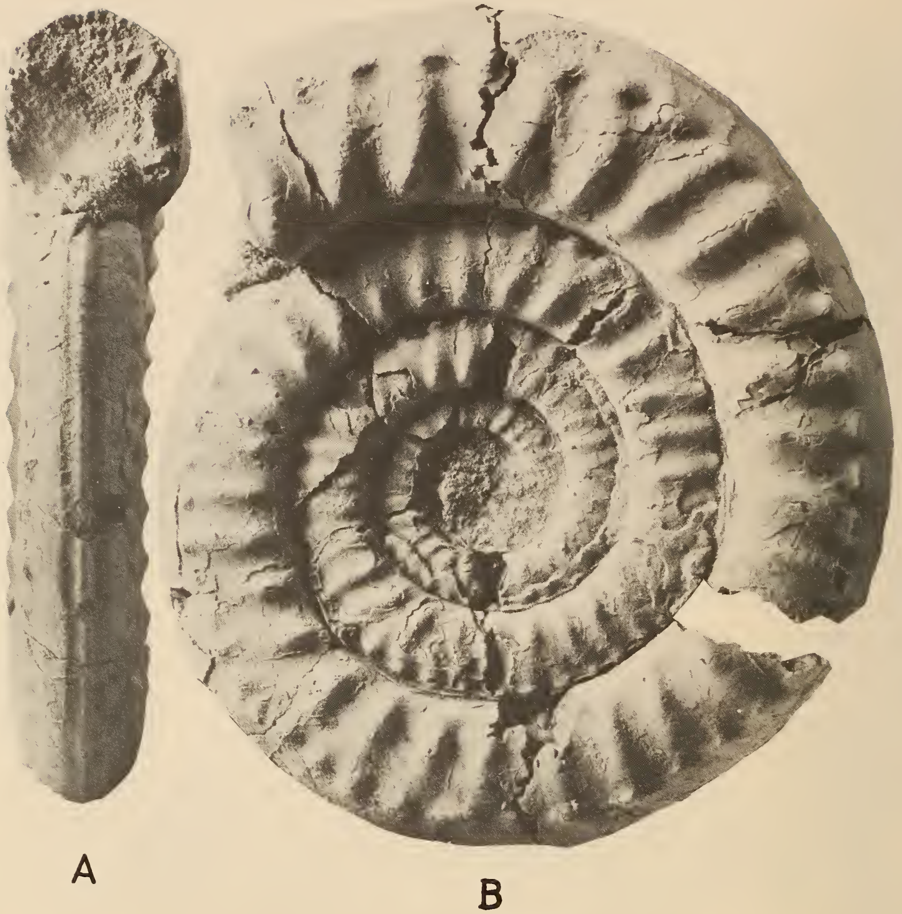

Fig. 21. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). SAS Z511, the holotype of Van Hoepen's *Peroniceras (Peroniceras) tenuis* (1965: 7, pl. 3, text-figs 1b, e); a compressed specimen representing the inner whorls of *P. (P.) subtricarinatum.* × 1. (See also Fig. 22.)

cause of prior usage of the combination *Ammonites tricarinata* by Poitiez & Michaud (1838). The syntypes survive in the D'Orbigny Collection (now in the Muséum Nationale d'Histoire Naturelle in Paris) under the catalogue number 7183. The larger of these, reillustrated here as Fig. 19A–B, D–E is herein designated lectotype of the species. It is from the environs of Sougraines, near Rennes-les-Bains (Aude).

Material

SAS Z1002, Z511, SAM–PCZ5943 from locality 93, hillslopes on the boundary of lots H101 and H102, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II, SAS Z1521 from locality 92, bulldozer scrapings

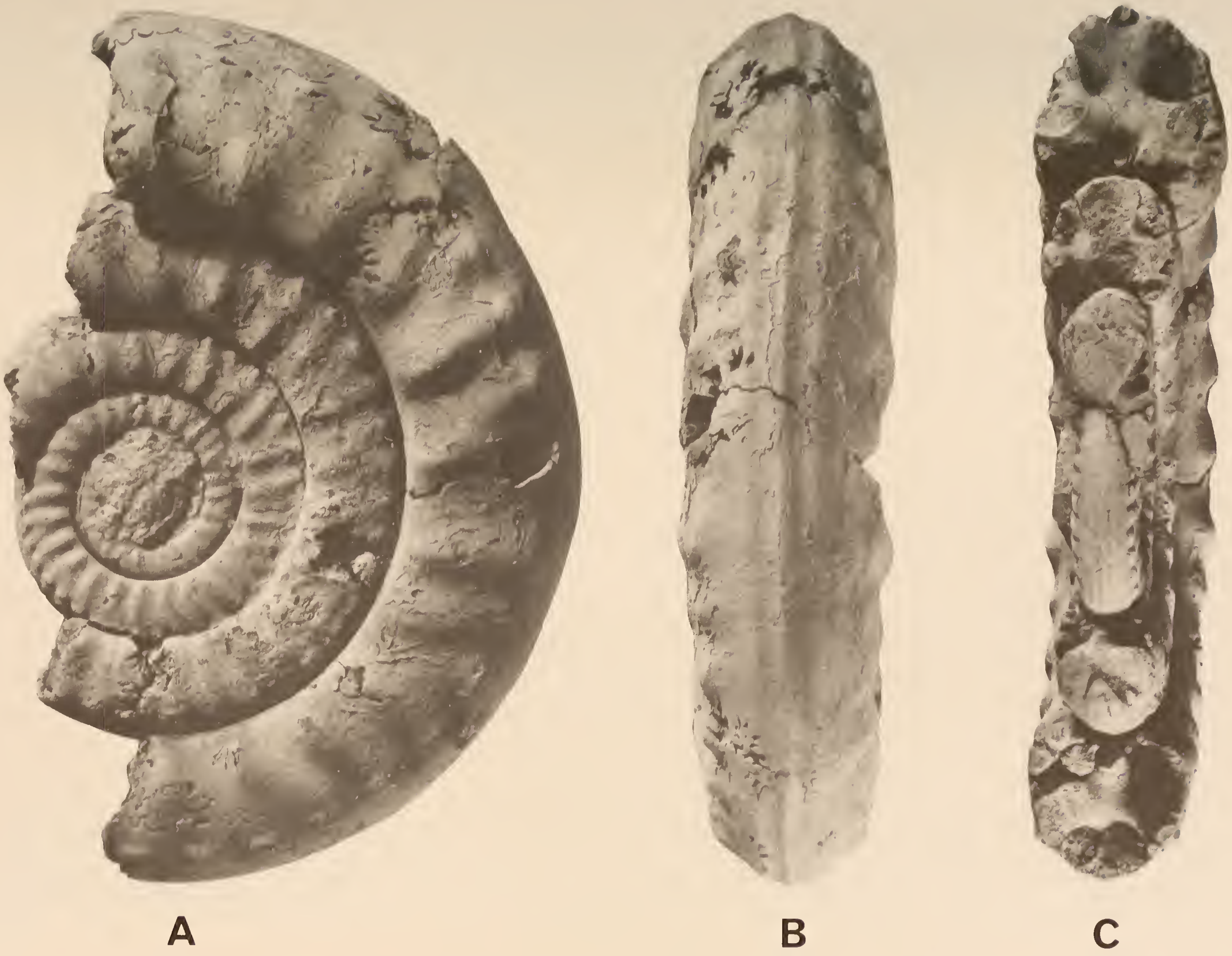

Fig. 22. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). SAM–PCZ5943, specimen with inner whorls similar to *P. (P.) tenuis* van Hoepen, 1965. × 0,6. (See Fig. 21.)

and adjacent hillslopes on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z511	132,0	37,0(28,0)	34,0(35,8)	1,08	73,0(55,3)	29:42
Z1002	152,0	33,0(21,7)	31,5(20,7)	1,05	92,0(60,2)	26:36
PCZ5943	195,0	40,0(20,5)	41.0(21.0)	0,97	113,0(57,9)	12×2:18×2
at	120,0	27,0(22,5)	'27,0(22,5)'	1,0	70,0(58,3)	14×2:19×2

Description

Coiling is polygyral and evolute with an umbilical diameter of 55 to 60 per cent of the total diameter. The adult whorl section is depressed, fastigiate with a prominent central keel and subordinate lateral keels and more or less parallel flanks in intercostal section. The dorsal zone of impression is very shallow and whorl overlap minimal. In the juvenile stage the whorl section is more rounded and the venter appears unicarinate. In costal section maximum width is across the dorsal third of the flanks.

Ornament consists of prominent rounded to bullate umbilical tubercles and smaller spirally elongated ventrolateral tubercles connected by weak ribs. Bifurcations are present both on the inner and outer whorls and in some cases one of the ribs of a bifurcating pair is weaker than the other, thus creating the appearance of intercalated ventrolateral tubercles. On the outer phragmocone whorls the umbilical tubercles may enlarge considerably and migrate away from the umbilical edge. Strength of ornament in the various specimens studied varies considerably as the figures show. In SAS Z511 (Fig. 21) faint spiral ornament is visible in the area between the ventral tubercles and the lateral keel.

The suture is finely subdivided. Details may vary considerably in response to position relative to ornamentation which affects mainly width and incision of the elements (Fig. 23).

Discussion

This species has been treated in various ways since its original description. De Grossouvre (1894: 94 et seq.) included Schlüter's *Ammonites tridorsatus* in the synonymy of *P. (P.) subtricarinatum*. According to De Grossouvre's interpretation they could, however, be separated at varietal rank. The typical *P. (P.) subtricarinatum* has a nearly equal number of single and bifurcating ribs, whereas *P. (P.) tridorsatum* has all the ribs simple. The lectotype of *P. (P.) subtricarinatum*, here refigured as Figure 19A–B, D–E shows D'Orbigny's figures to be considerably restored, especially as far as the inner whorls are concerned. The specimen does, however, show the typical common and distinctive bifurcations on the outer whorls.

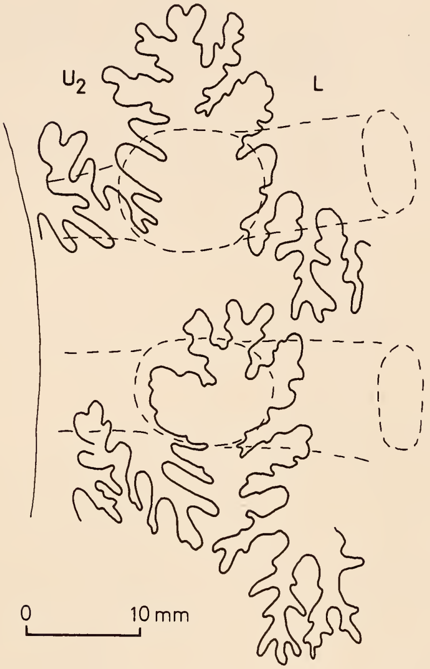

Fig. 23. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850). Two successive sutures of SAS Z1002 to illustrate influence of ornament on details of suture, in this case especially the width of the stem of saddle L/U_2.

Desio's (1920: 206, pl. 25 (fig. 3)) *P. subtricarinatum* var. *etruscum* has weak ornament on the inner whorls, and lacks umbilical tuberculation on the outer whorls. Furthermore, the whorl section is much higher than wide. As Desio (1920: 207) pointed out, the specimen is very close to *P. (P.) dravidicum*.

P. cf. *subtricarinatum* var. *tridorsatum* of Desio (1920: 205, pl. 12 (fig. 10)) is poorly preserved, but because of the single ribbing falls beyond the limits of this species.

P. (P.) tenuis van Hoepen (1965: 7, pl. 3, text-figs 1b–e) merely represents the inner whorls of a weakly ornamented form of *P. (P.) subtricarinatum* as Figures 21–22 show, and is thus included in the synonomy.

P. haasi Young (1963: 72, pl. 34 (figs 3–4), pl. 35 (figs 1–2)) from the Coniacian of Texas has the general appearance of *P. (P.) subtricarinatum* but weaker ornament. Given more material it might be possible to include it in the strict synonomy of *P. (P.) subtricarinatum*, as was done with *P. (P.) tenuis* van Hoepen.

Occurrence

Middle Coniacian *P. (P.) tridorsatum* Zone of western and central Europe, north Africa, Madagascar, and Mexico. Coniacian II and III of Zululand.

Peroniceras (Peroniceras) westphalicum (von Strombeck, 1859)

Figs 24–28

Ammonites westphalicus von Strombeck, 1859: 56. Schlüter, 1867: 30, pl. 6 (fig. 2); 1872: 45, pl. 13 (figs 5–6).
Peroniceras westphalicum (Schlüter): de Grossouvre, 1894: 98, pl. 12 (figs 1, 4), text-fig. 38. Pruvost, 1910: 366. *Non* Scupin, 1913: 94, pl. 4 (fig. 8). Desio, 1920: 214, pl. 12 (fig. 2), pl. 13 (fig. 3). Diener, 1925: 152. Adkins, 1933: 407, 453. ? Andert, 1934: 407. Young, 1963: 74, pl. 28 (figs 2–4), pl. 29 (figs 1–2), text-fig. 15d. Collignon, 1965: 60, pl. 440 (fig. 1807).
Peroniceras westphalicum (Schlüter) var. *australis* Venzo, 1936: 100, pl. 9 (fig. 4), pl. 11 (fig. 8).
Peroniceras stephaninii Venzo, 1936: 102, pl. 9 (fig. 3), pl. 11 (fig. 10).
Peroniceras guerini Collignon, 1965: 64, pl. 442 (fig. 1811).
Peroniceras cf. *westphalicum* (Schlüter), 1867: Amedro & Robaszynski, 1978: 37, pl. 1 (fig. 1).
? Peroniceras latum Matsumoto & Muramoto, 1981: 52, pl. 6 (fig. 1), pl. 7 (fig. 1), text-fig. 1.

Type specimens

Von Strombeck's originals, from the Coniacian of Westphalia, have not been traced. They were presumably in Berlin.

Material

NMB D1146, D1145, D1060, SAS A2941, A1972, all from locality 72, degraded river cliffs on the northern banks of the Mzinene River downstream of the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1616 from locality 93, bulldozer scrapings and adjacent hillslopes around the pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z696	144,0	41,0(28,4)	43,0(29,8)	0,95	85,0(59,0)	15×2:16×2
A1972	155,0	35,0(22,5)	40,0(25,8)	0,87	89,0(57,4)	—
Z1616	195,0	—	50,0(25,6)	—	100,0(51,2)	16×2:16×2
D1146	195,0	49,0(25,2)	56,0(28,0)	0,87	97,0(49,7)	21:21

Description

Coiling is evolute with an umbilical diameter of about 50 to 60 per cent of the total diameter. The whorl section is compressed throughout, higher than wide with little-inflated flanks, and has a very low umbilical wall and broadly rounded venter.

Ornament on the inner whorls is more or less of the *P. (P.) dravidicum* type with frequently bifurcating ribs, though not as strongly developed as in the latter species. With increasing diameter the umbilical tubercles become progressively weaker, and eventually lateral ornament consists of broad, low ribs that end or weaken considerably before reaching the clavate ventrolateral tubercles. At the same time there is a tendency towards a decrease in the number of bifurcations. On the outer whorls of the specimens available, virtually all ribs are single. Detail of the ornament varies considerably, from densely costate as in SAS Z1616 (Fig. 27) to sparsely costate in NMB D1146 (Fig. 24).

The species may grow to a very large size. The suture is highly incised (Fig. 28).

Discussion

In the absence of type specimens, interpretation of this species presents difficulties. It is here interpreted in terms of the specimen from near Altenessen

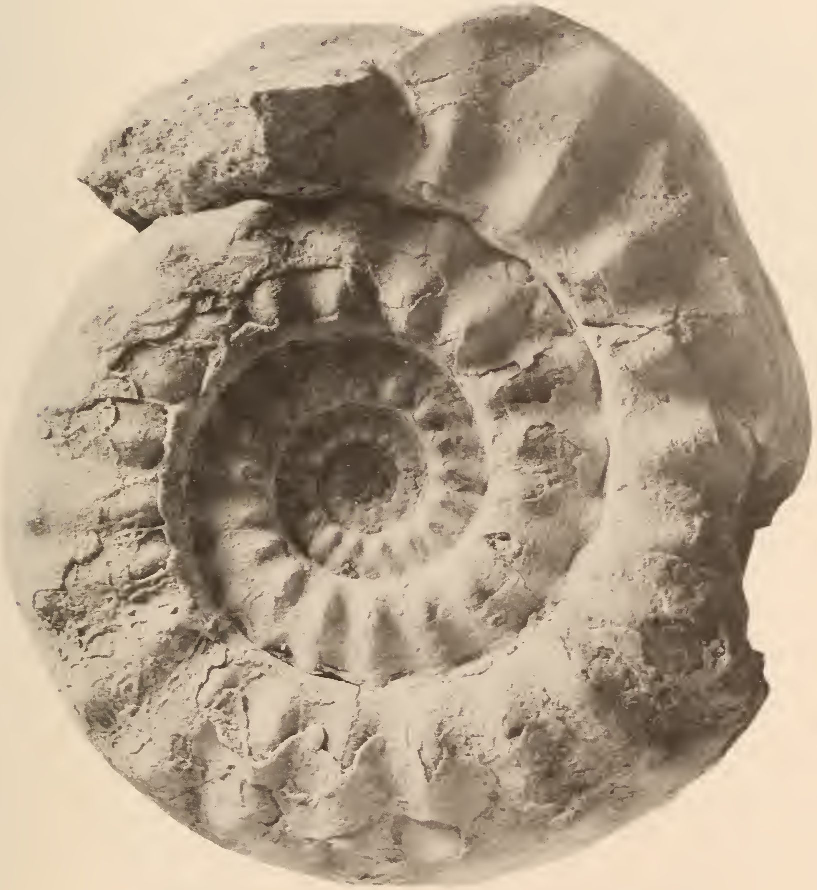

Fig. 24. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). NMB D1146, specimen with typical ornament consisting of low, broad ribs. × 0,6.

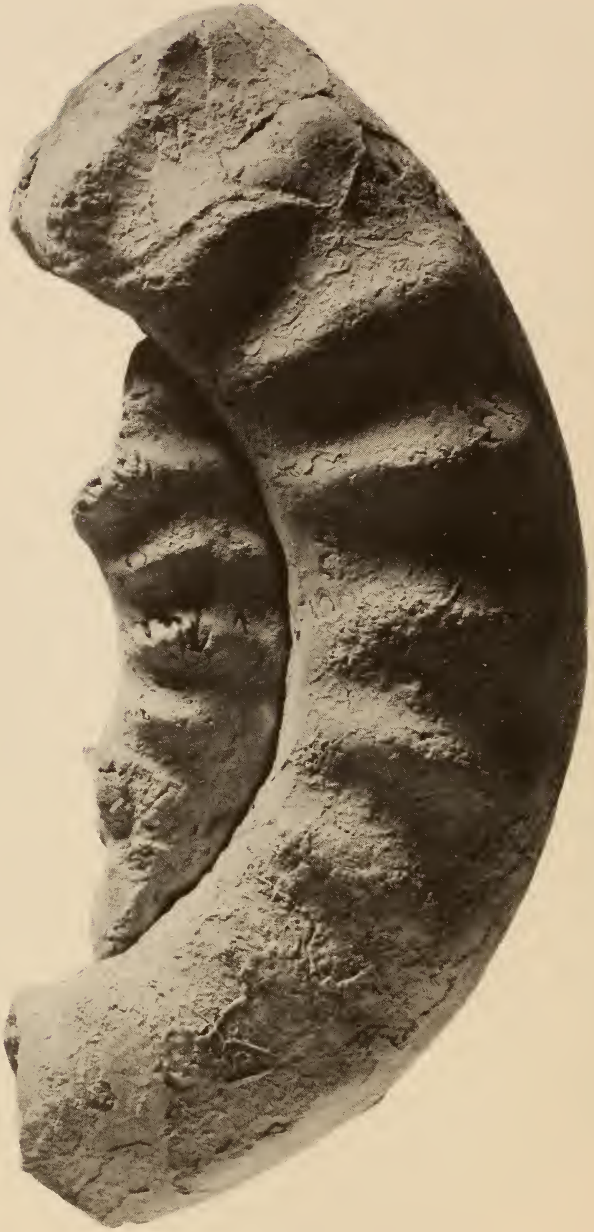

Fig. 25. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). NMB D1060. Evolute specimen with typical ornament. × 0,69.

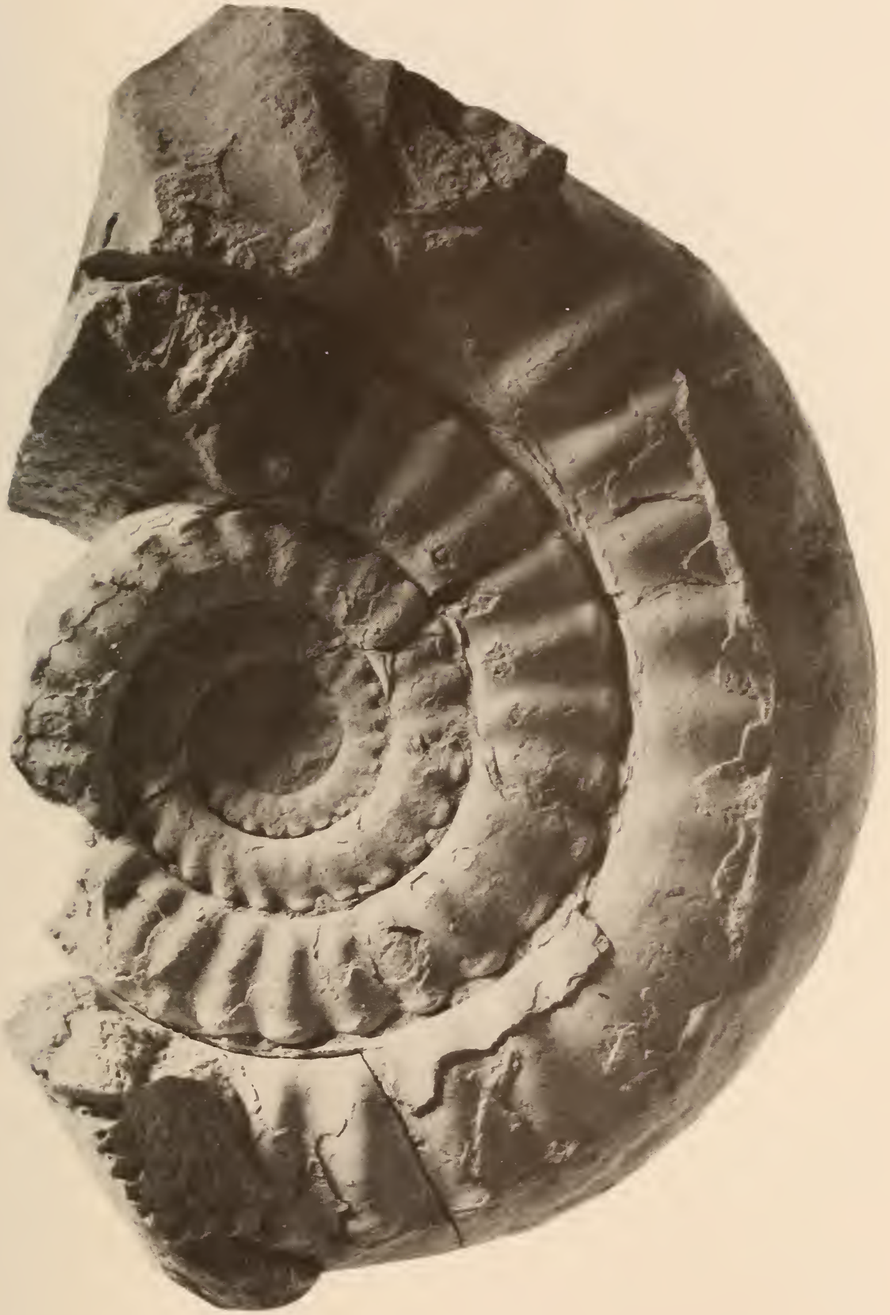

Fig. 26. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). SAS Z696, specimen with ornament approaching that of *P. (P.) dravidicum* Kossmat, 1895. × 0.77.

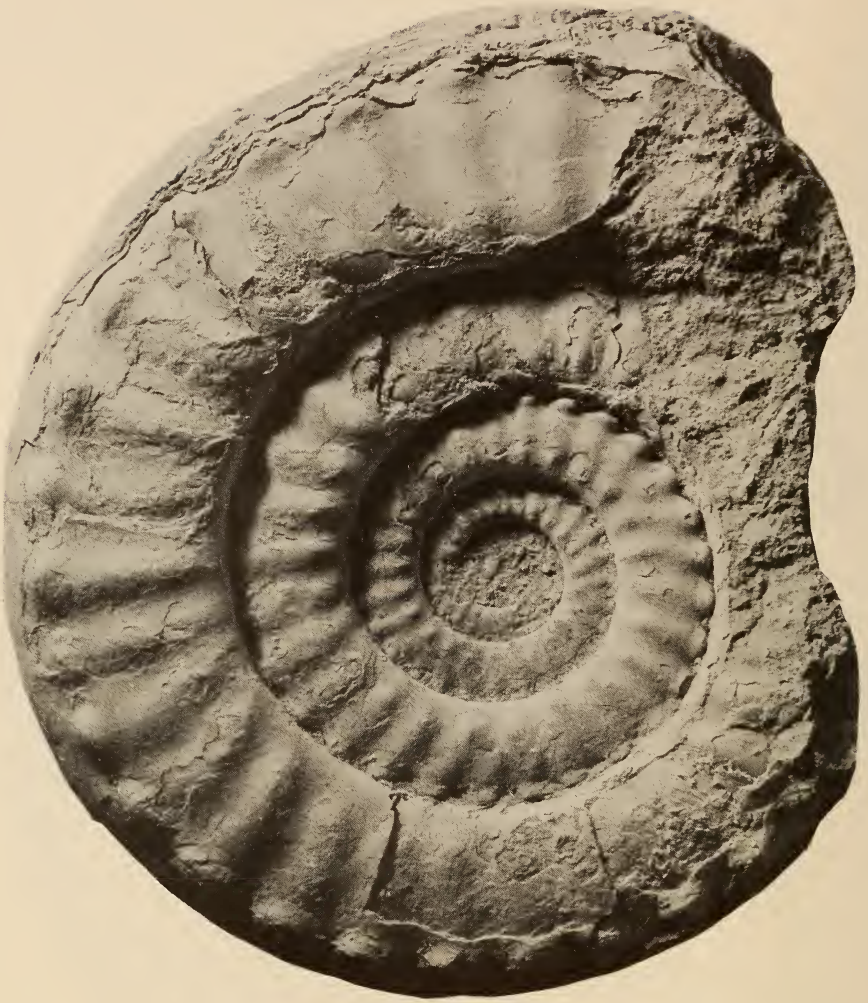

Fig. 27. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). SAS Z1616, specimen with ornament transitional to *P. (P.) dravidicum* Kossmat, 1895. × 0,70.

figured by Schlüter (1872, pl. 13 (figs 5–6)). This clearly shows the low, rounded and broad bullae, which clearly distinguish the species from the majority of other peroniceratids.

One of the specimens figured by De Grossouvre (1894, pl. 12 (fig. 1)), from the Craie de Villedieu of Touraine, lacks the typical broad lateral ornament and may possibly be a transition towards *P. (P.) subtricarinatum.*

P. westphalicum var. *italicum* Desio (1920: 216, pl. 16 (fig. 4)) lacks the bullae of typical *P. (P.) westphalicum* and has, instead, sharp-crested, narrow, widely spaced lateral ribs. In this respect it bears resemblance to *P. stefaninii*

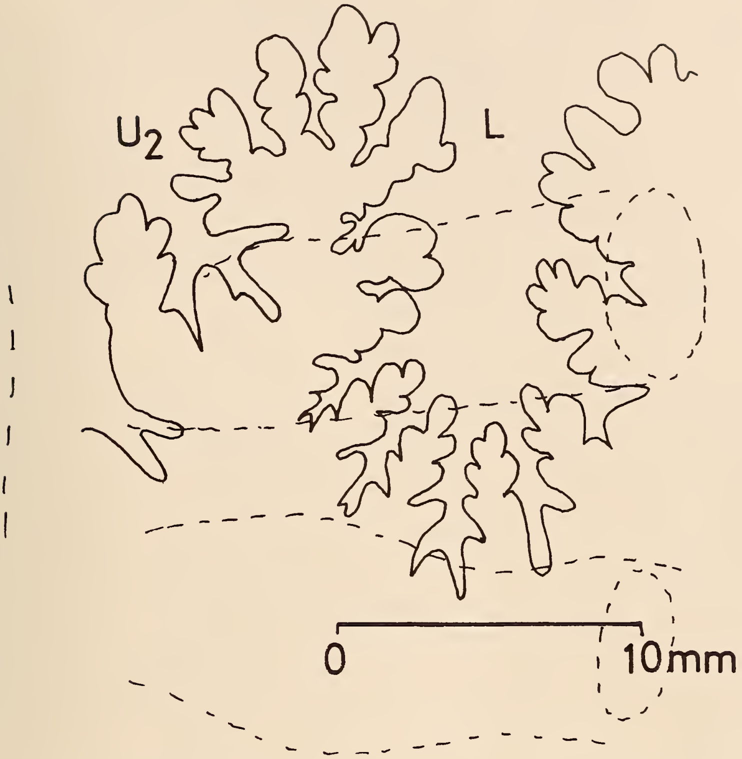

Fig. 28. *Peroniceras (Peroniceras) westphalicum* (von Strombeck, 1859). Partial suture-line of SAS Z996.

Venzo (1936: 102, pl. 9 (fig. 3)) from the Coniacian of Zululand. Specimen NMB D1146 (Fig. 24) also shows a tendency towards narrowing of the ribs as in these forms. They may thus safely be included in the strict synonomy of *P. (P.) westphalicum*, in contrast to the conclusions of Matsumoto & Muramoto (1981: 55).

P. westphalicum var. *australis* Venzo (1936: 100, pl. 5 (fig. 4)), also from the Coniacian of Zululand, resembles the specimen figured by De Grossouvre (mentioned above) in having a rather prominent umbilical tubercle and a more quadrate whorl section than typical *P. (P.) westphalicum.* It is morphologically transitional to *P. (P.) subtricarinatum*.

P. guerini Collignon (1965: 64, pl. 442 (fig. 1811)) has typical *P. (P.) westphalicum* ornament, and differs only in possessing a prominent depression separating the lateral ribs from the ventrolateral tubercles. The authors doubt if this feature merits specific separation, and include the species in the strict synonomy of *P. (P.) westphalicum.*

P. latum Matsumoto & Muramoto (1981: 52, pl. 6 (fig. 1), pl. 7 (fig. 1), text-fig. 1) was considered to be a close ally of *P. stefaninii* Venzo, 1936, differing only in a wider umbilicus (U = 63 %) and numerous (twenty-eight) ribs on the outer whorl. It is also a probable synonym of the present species.

Occurrence

Middle Coniacian of western Europe, Madagascar, Zululand, and the Gulf Coast of North America.

Peroniceras (Peroniceras) dravidicum Kossmat, 1895

Figs 29–42

Ammonites subtricarinatus d'Orbigny: Stoliczka, 1865: 54, pl. 31 (fig. 3)
Schloenbachia (Peroniceras) dravidica Kossmat, 1895: 190, pl. 22 (fig. 3).
Peroniceras dravidicum Kossmat: Solger, 1904: 181, figs 71–72. Lombard, 1930: 294, pl. 30 (fig.1). Venzo, 1936: 99, pl. 10 (fig. 1), pl. 11 (fig. 9). *Non* Ciry, 1940: 212. Reyment, 1958: 65. Collignon, 1965: 52, pl. 436 (fig. 1802), p. 62, pl. 441 (fig. 1809); 1978: 63, pl. 28 (fig. 1).
Peroniceras cfr. *subtricarinatum* d'Orbigny var. *dravidicum* Kossmat: Desio, 1920: 207, pl. 12 (fig. 9).
Peroniceras cf. *dravidicum* Kossmat: Spath, 1921: 295, pl. 23 (fig. 1).
Peroniceras sp. aff. *dravidicum* Kossmat: Collignon, 1967: 51, pl. 30 (fig. 6).
Peroniceras platycostatum van Hoepen, 1955: 367, figs 15–17.
Peroniceras spathi van Hoepen, 1955: 368.
Peroniceras (Peroniceras) multinodatum van Hoepen, 1965: 8, pl. 4; text-fig. 1f.
Peroniceras (Zuluiceras) obliquenodatum van Hoepen, 1965: 14, pl. 8; text-fig. 3f.
Peroniceras (Zuluiceras) bessiae van Hoepen, 1965: 18, pl. 13.

Type specimen

The lectotype is the original of Kossmat (1895, pl. 23 (fig. 3a–d)) by the subsequent designation of Matsumoto (1965: 213).

Material

SAS A536, Z253, Z753, Z1017, SAM–PCZ5944, PCZ5495, K5494, K4950, NMB D2145b, D1148 from locality 72, degraded river cliff and northern banks of the Mzinene River downstream from the junction with the Munywana River, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z663, Z811, Z1607, Z1521, Z1521c, Z1616, Z1632, Z1650, Z1662, Z1672, Z1674 from locality 92, bulldozer scrapings and adjacent hillslopes around the pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS Z1 and Z892 from locality 93, hillslopes on either side of the boundary fence separating lots H101 and H102, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II and III. SAS A609 from locality 24, caisson excavations for new Nyalazi River bridge, Zululand, St. Lucia Formation, inferred to be Coniacian II and III. Numerous fragments and uncatalogued material from the above localities.

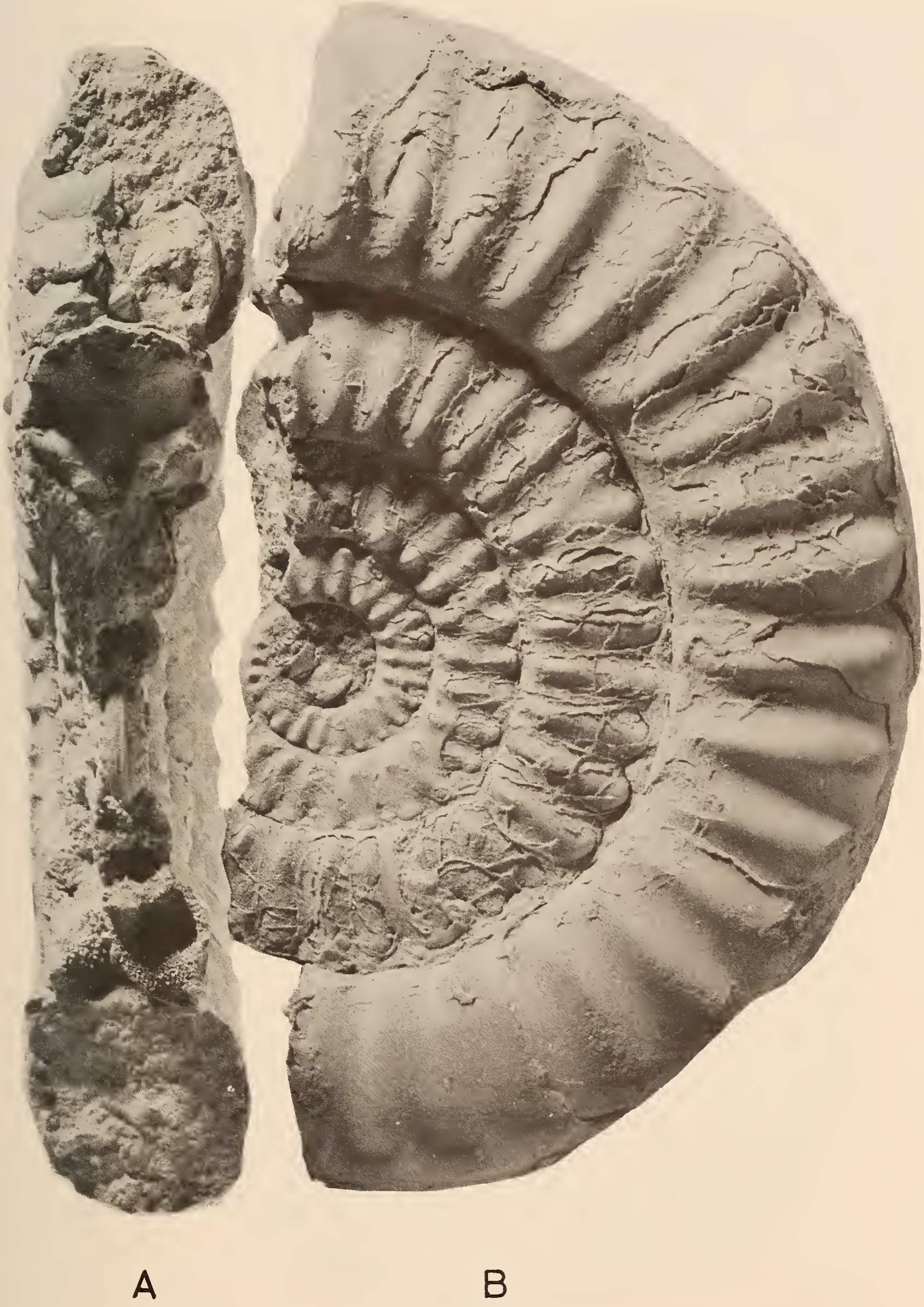

Fig. 29. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1017 showing details of ontogeny up to the body chamber. Note especially the unicarinate venter on the inner whorls. × 0,9.

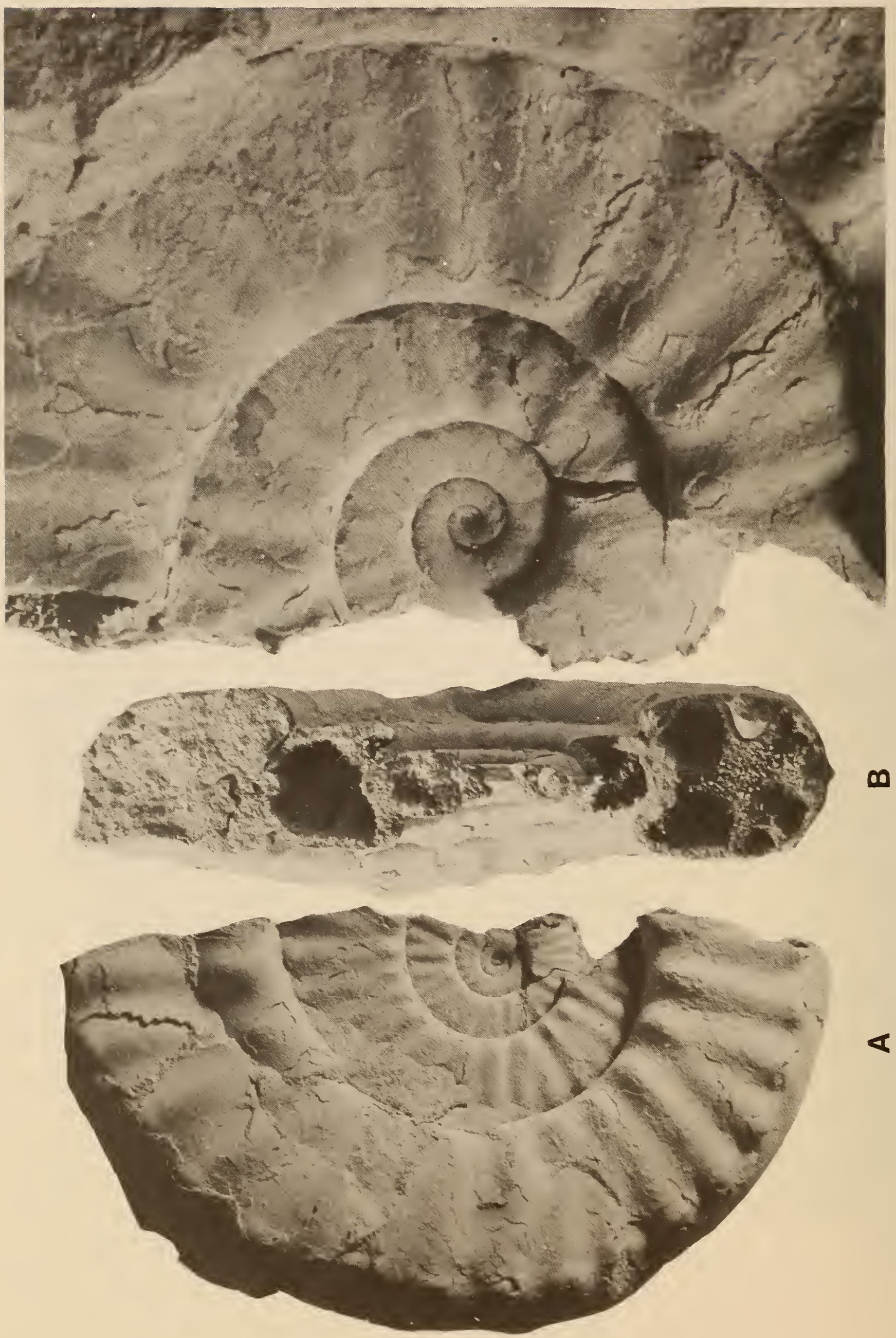

Fig. 30. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS PCZ5945 showing details of ontogeny. Note especially the smooth, unicarinate inner whorls. A–B × 1, C × 3.

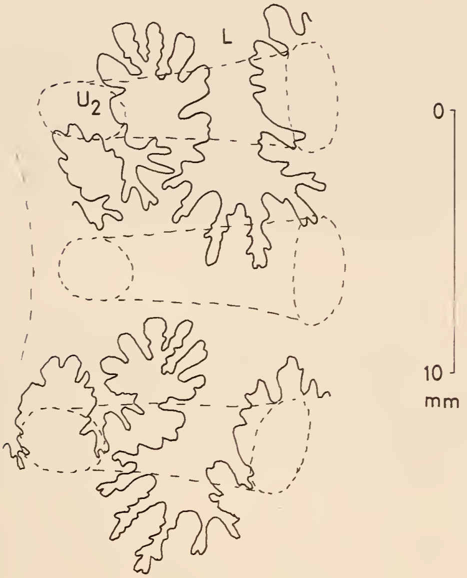

Fig. 31. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1633 partial suture-line showing effect of ornamentation on details of elements, in this case saddle U_2/U_3.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
D1148	44,0	11,0(25,0)	14,0(31,8)	0,79	19,0(43,2)	19:30
Z1607	46,0	13,0(28,3)	14,0(30,4)	0,92	21,0(45,6)	19:24
Z1672	46,0	12,0(26,1)	13,1(28,3)	0,92	23,0(50,0)	27:38
Z253	65,0	18,0(27,7)	21,0(32,3)	0,86	29,0(44,6)	20:32
Z892	74,0	20,0(27,0)	21,0(28,4)	0,95	37,0(50,0)	—
Z811	75,0	24,0(32,0)	24,0(32.0)	1.0	34,0(45,3)	26:29
K5494	78,0	20,0(25,6)	24,0(30,8)	0,83	37,0(47,4)	20:34
Z1632	80,0	20,0(25,0)	23,0(28,7)	0,87	40,0(50,0)	23:27
Z1662	80,0	19,0(23,7)	23,0(28,7)	0,83	39,0(48,8)	20:31
Z663	81,0	18,0(22,2)	29,0(35,8)	0,62	39,0(48,1)	15:34
Z1521	82,0	20,0(24,4)	25,0(30,5)	0,80	37,0(45,1)	24:35
A536	87,0	22,0(25,3)	27,0(31,0)	0,81	39,0(44,8)	20:36
Z1521c	87,0	22,0(25,3)	27,0(31.0)	0,82	40,0(45,9)	18:24
PCZ5944	97,0	26,0(26,8)	25,0(25,8)	1,04	51,0(52,6)	23:31
D1145b	104,0	29,0(27,9)	29,0(27,9)	1,0	54,0(51,9)	20:26
D1145a	116,0	33,0(28,5)	34,0(29,3)	0,97	57,0(49,1)	26:32
A912	122,0	31,0(25,4)	32,0(26,2)	0,97	66,0(54,1)	34:34

	D	*Wb*	*Wh*	*Wb*/*Wh*	*U*	*R*
Z753	124,0	31,0(25,0)	41,0(33,1)	0,75	55,0(44,3)	—
Z1616	141,0	38,0(26,9)	45,0(31,9)	0,84	62,0(43,9)	20:35
Z1674	151,0	37,0(24,5)	49,0(32,5)	0,75	72,0(47,7)	29:29
PZ5495	150,0	35,0(23,3)	37,0(24,7)	0,95	83,0(55,3)	28:35
Z1017	183,0	—	45,0(24,6)	—	104,0(56,8)	37:37
Z1650	203,0	—	55,0(27,1)	—	114,0(56,1)	34:34

Description

This is the largest known collection of *P. (P.) dravidicum*, and exhibits all stages of ontogeny, as well as the extensive intraspecific variation.

Coiling is generally evolute, the umbilicus comprising up to 56 per cent of the diameter in large individuals, but it may be as low as 43 per cent in smaller specimens and what appear to be stratigraphically younger representatives of the species.

The whorl section is generally rectangular, higher than wide throughout, but may be quadrate or even slightly wider than high in some individuals.

Details of the early ontogeny can be seen in SAS Z1017 (Fig. 29), NMB D1148 and SAM–PCZ5945 (Fig. 30). The early whorls are smooth, with parallel flanks converging to an acute, unicarinate venter. The smooth stage lasts up to about 8 mm, whereafter rounded tubercles start appearing at the umbilical edge and clavate ventrolateral ones in the umbilical suture of the succeeding whorl. They are connected by weak, inconspicuous bifurcating and single ribs. This ornament remains basically the same thoughout, except on the later part of the phragmocone and on the body chamber of the larger specimens, where the ribs become more club-shaped and predominantly single, and the umbilical tubercles become indistinct. This latter ornament is very reminiscent of *P. (P.) westphalicum*.

The central keel is strongest throughout ontogeny.

The suture-line is complex, generally with highly incised elements. Details differ, however, according to the relative position of the sutural elements to ornament (Fig. 31). If saddles coincide with tubercles, they tend to be rather broad, whereas if situated in the interspaces, they are narrow-stemmed as in typical *Peroniceras*. The attachment of the U_2/U_3 saddle to the base of the saddle L/U_2 is prominent in the species.

Discussion

Specimens referred to this species form the bulk of the *Peroniceras* material before us. Variants show gradations in some characters, both in contemporary and successive populations, towards other species. It is easily recognized, however, by the numerous bifurcating ribs on the inner whorls, compressed rectangular whorl section, evolute coiling and weak lateral keels.

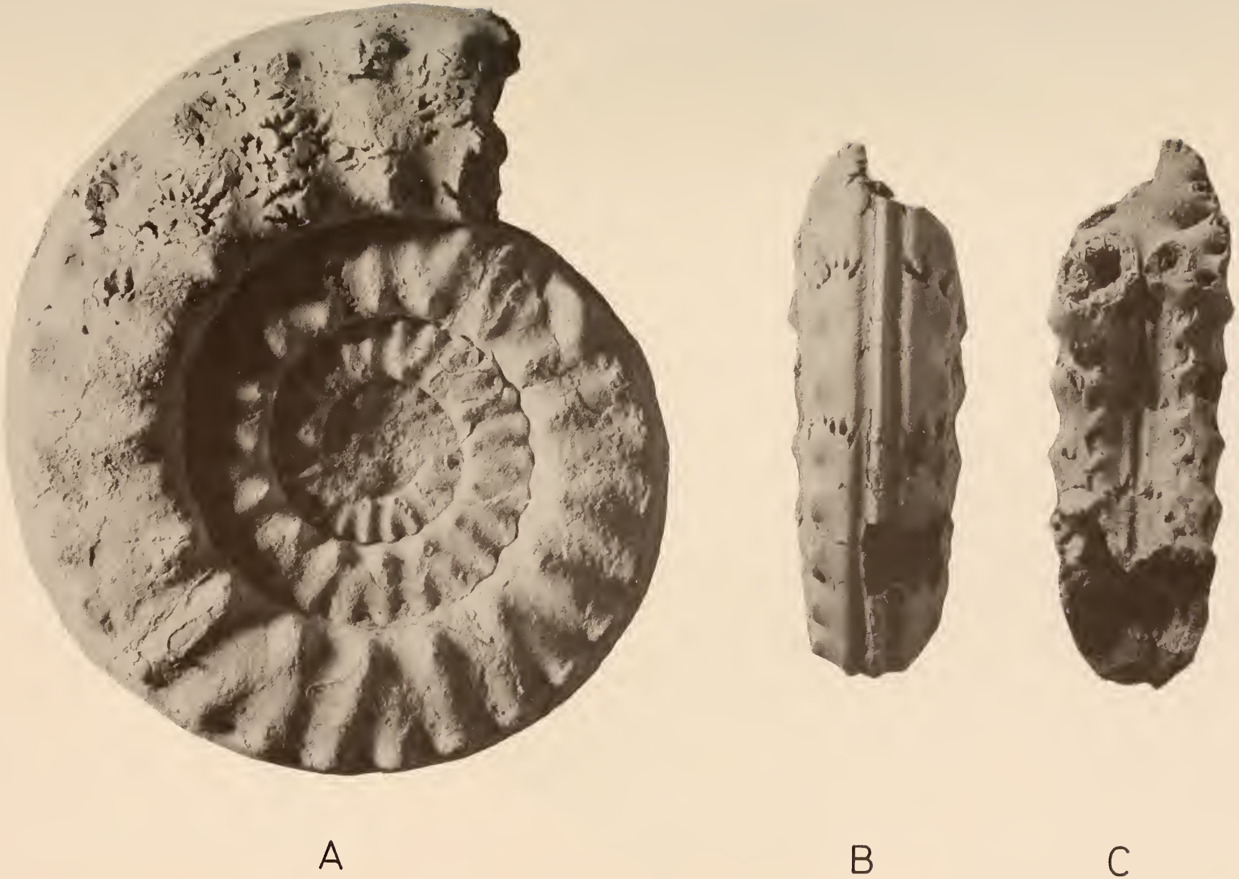

Fig. 32. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. A. SAM–PCZ5946. B–C. The specimen figured and described by Spath (1921: 295, pl. 23 (figs 1a–d)) as *Peroniceras* cf. *dravidicum*, and named *Peroniceras spathi* by Van Hoepen (1955: 368). All × 1.

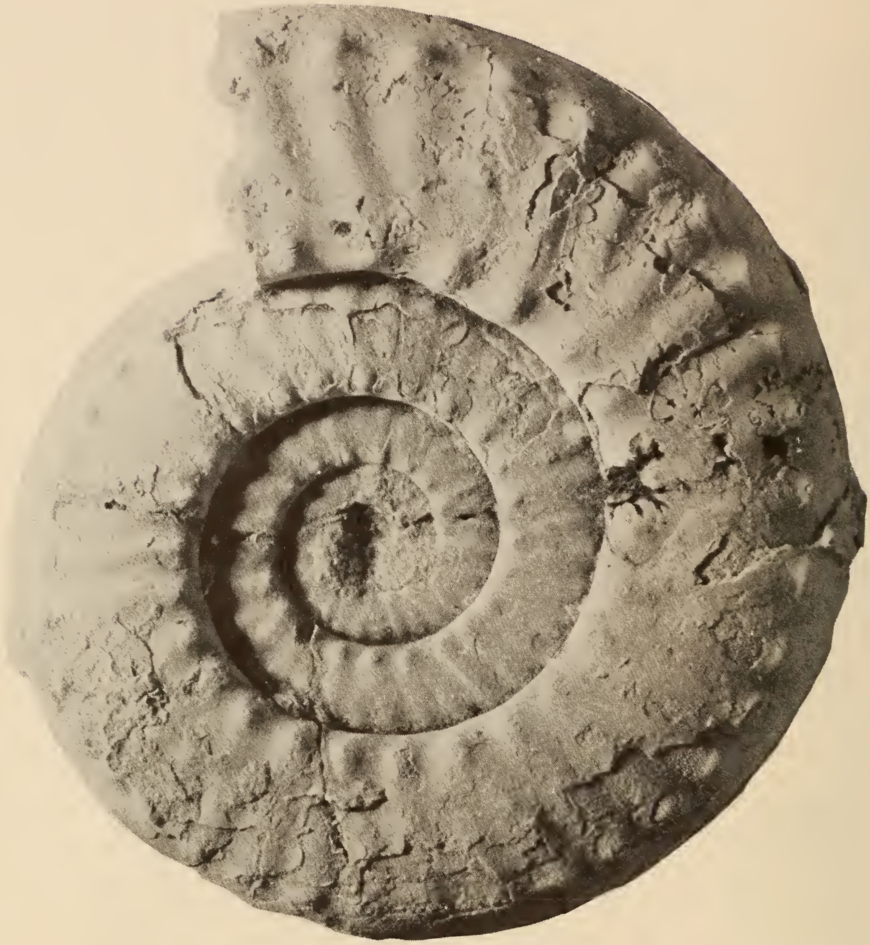

Fig. 33. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1, the holotype of *P. (P.) platycostatum* van Hoepen, 1955. This is merely a compressed variety of *P. (P.) dravidicum*. × 1.

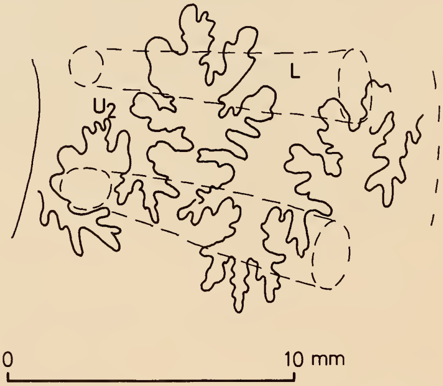

Fig. 34. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. Suture-line of SAS Z1119.

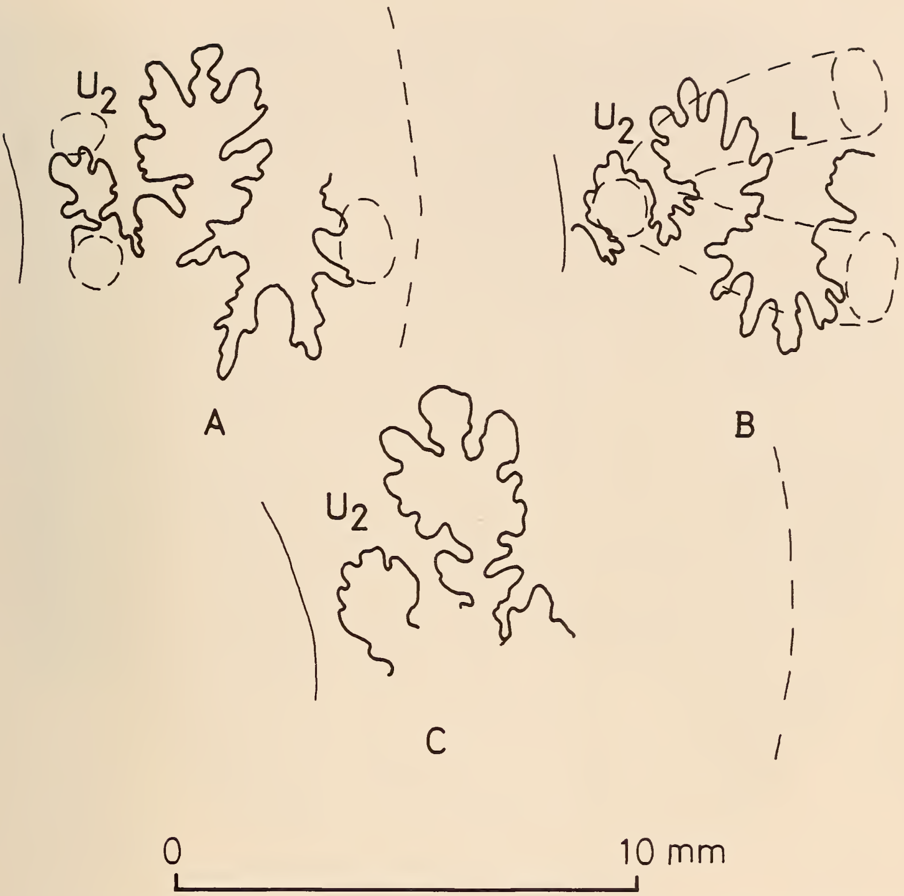

Fig. 35. *Peroniceras (P.) dravidicum* Kossmat, 1895. Suture-lines of juvenile specimens. A. SAS Z1633. B. SAS Z1615. C. Uncatalogued fragment.

A number of species described by Van Hoepen (1955, 1965) are here regarded as synonyms of this species. *Peroniceras spathi* van Hoepen (1955: 368 = *Peroniceras* cf. *dravidicum* Stoliczka of Spath, 1921: 295, pl. 23 (fig. 1a–d)) (Fig. 32B–C herein) is clearly a synonym of *P. (P.) dravidicum. P. platycostatum* van Hoepen (1955: 367, figs 15–17) (Fig. 33 herein) was said to differ from *P. (P.) dravidicum* in having slightly converging flanks and somewhat differently disposed umbilical and ventrolateral tubercles. Van Hoepen also considered his species to differ from the specimen of *P. (P.) dravidicum* figured by Venzo (1936, pl. 10 (fig. 1), pl. 11 (fig. 2)) on the basis of the denser ribbing and higher whorl section. Given the variation shown by the material at the authors disposal, these differences are obviously within the limits of intraspecific variation, and *P. platycostatum* is included in the strict synonymy of *P. (P.) dravidicum*.

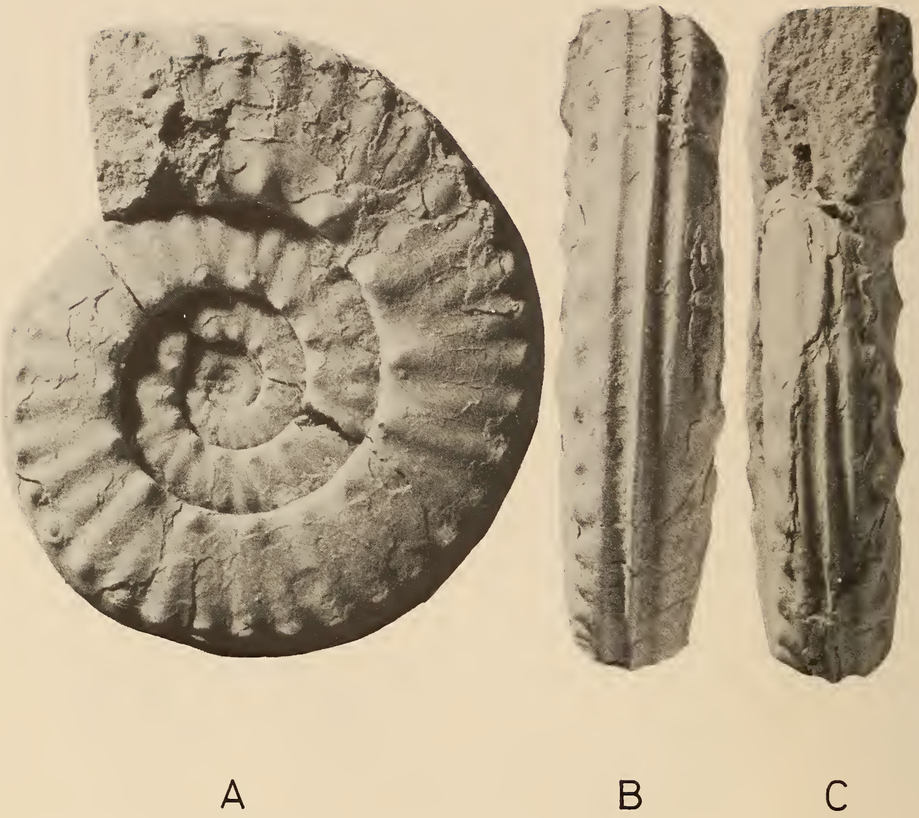

Fig. 36. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z663, the holotype of Van Hoepen's *P. (P.) multinodatum*. × 1.

P. (P.) multinodatum van Hoepen (1965: 8, pl. 4, text-fig. 1f) (Fig. 36 herein) differs from the commoner forms of *P. (P.) dravidicum* in having an unusually high ratio of ventral to umbilical tubercles (34:15), but has all the other characteristics of the species.

P. (Zuluiceras) obliquenodatum van Hoepen (1965: 14, pl. 8, text-fig. 3f) (Fig. 37 herein) is nothing more than a coarsely ornamented variant of *P. (P.) dravidicum*, although the narrow umbilical width (45%) suggests that it is in this respect transitional to *P. (Zuluiceras)*. Another form transitional to *P. (Zuluiceras)*, but which still falls within the limits of *P. (P.) dravidicum*, is *P. (Zuluiceras) bessiae* van Hoepen (1965: 18, pl. 13) (Fig. 38 herein).

Some of the very large forms of *P. (P.) dravidicum* here figured (e.g. Figs 39–40, with very evolute whorls and club-like, simple ribs on the outer whorls, are reminiscent of *P. (P.) westphalicum*. In typical *P. (P.) westphalicum*, however, the ribs are broad and widely spaced. The inner whorls of both species are remarkably similar, suggesting a close relationship.

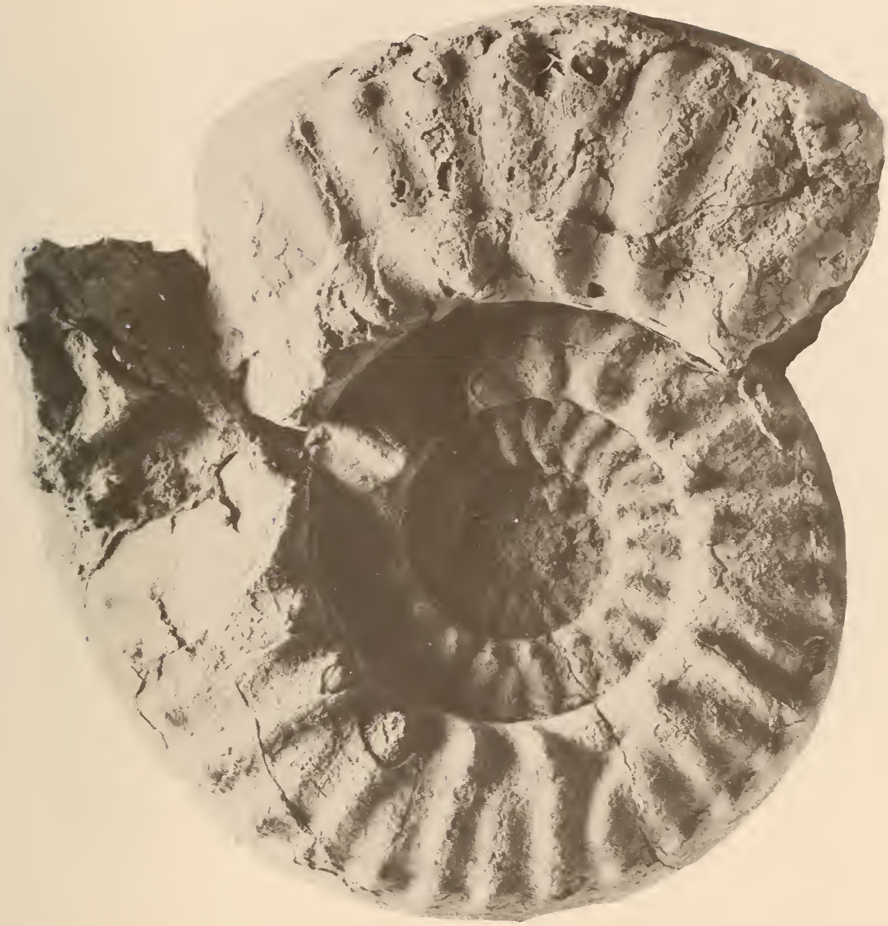

Fig. 37. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z753, the holotype of *P. (Zuluiceras) obliquenodatum* van Hoepen, 1965. This specimen is transitional to subgenus *P. (Zuluiceras)*. × 1.

Specimens of *P. (P.) dravidicum* with more quadrate whorl sections and stronger ornament are in these respects transitional to *P. (P.) subtricarinatum*, e.g. SAS A609 and SAM–PCZ5946 (Fig. 32A). Typically, however, *P. (P.) subtricarinatum* has a quadrate to depressed whorl section with very strong umbilical bullae. In addition, the venter is generally more rounded and the coiling more evolute.

P. (P.) dravidicum is the ancestor of *P. (Zuluiceras)*. The transition involved the development of tighter coiling, retention of a single keel to greater diameters, and more prominent development of rounded ribbing on the outer whorls (Fig. 41). In fact, one of the paratypes of *P. (Z.) zulu*, SAS Z14 (Fig. 45), is still very close to *P. (P.) dravidicum*.

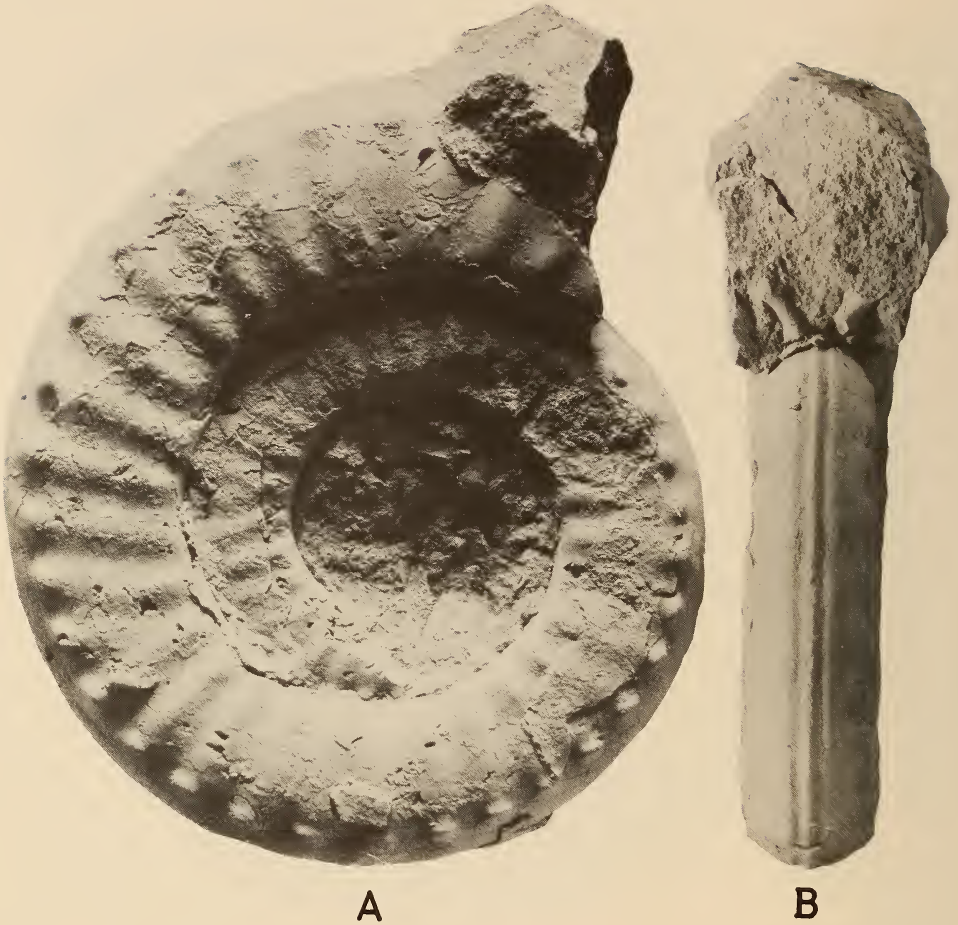

Fig. 38. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z255, the holotype of *P. (Zuluiceras) bessiae* van Hoepen, 1965, another specimen transitional to subgenus *P. (Zuluiceras)*. × 1.

In addition to the above changes, there appears to have been a general increase in overall size.

Occurrence

Coniacian of Italy, north, west and central Africa, Madagascar and India, Coniacian II and III of Zululand.

Subgenus *Peroniceras (Zuluiceras)* van Hoepen, 1965

(= *Zuluites* van Hoepen, 1965: 23; *Sornayceras* Matsumoto, 1965: 226)

Type species

Peroniceras (Zuluiceras) zulu van Hoepen, 1965: 23, by original designation.

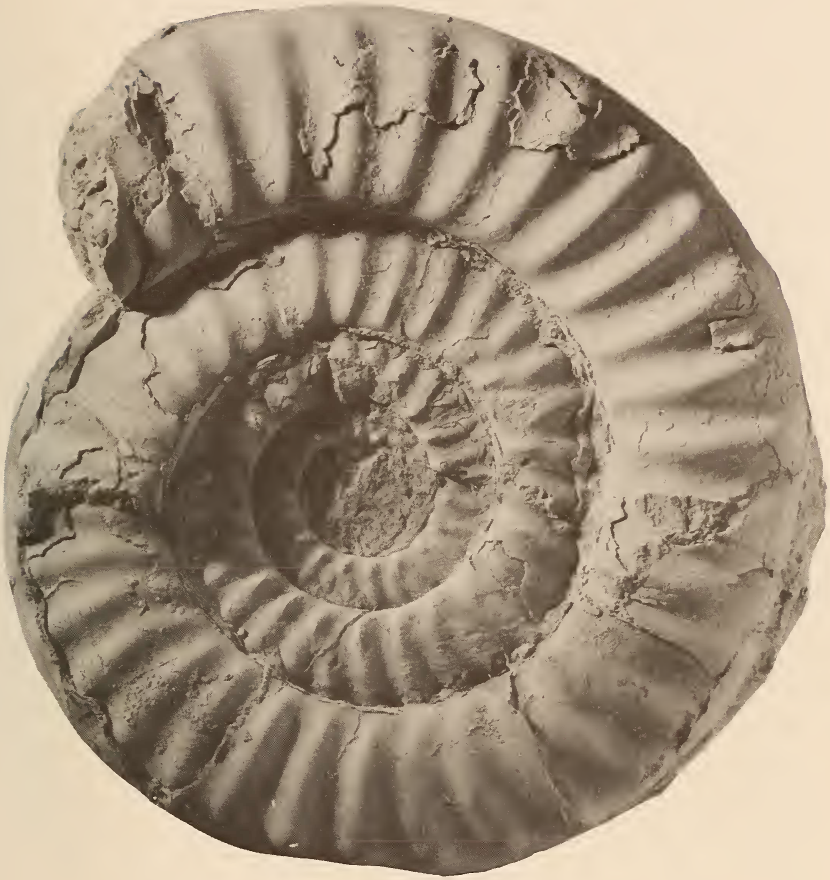

Fig. 39. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1650, a large form with club-like simple ribs on outer whorls. × 0,6.

Diagnosis

Progressively more involute than *Peroniceras (Peroniceras)* with adult whorls tending to become rounded and smooth. Lateral keels are weak to absent on outer whorls and siphonal keel may be entire or serrated. Suture complex, of *P. (P.) dravidicum* type.

Discussion

Van Hoepen separated *P. (Zuluiceras)* from *P. (Zuluites)* on the basis of the greater involution and loss of ornament in adults of the latter. Stratigraphic work shows that there is a progression from early, relatively evolute Middle Coniacian species with persistent ornament that are close to *Peroniceas (Peroniceras)* (e.g. *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873),

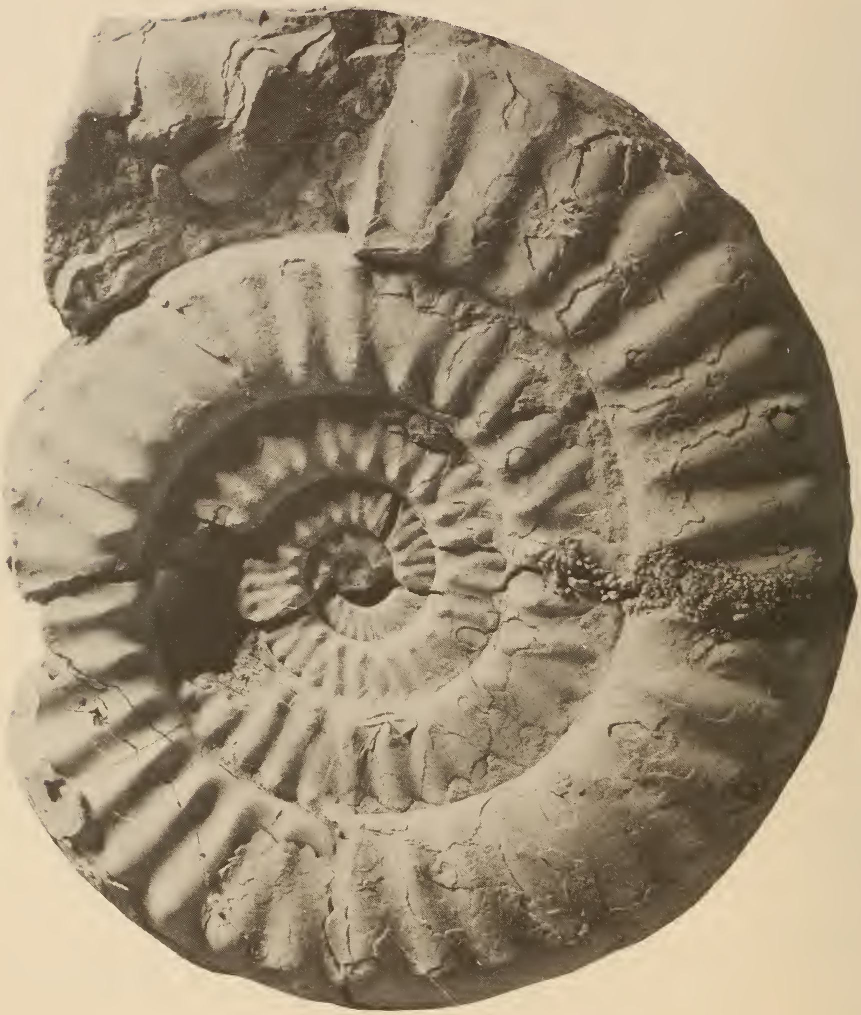

Fig. 40. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1663 a large form with club-like ribs on outer whorls. × 0,84.

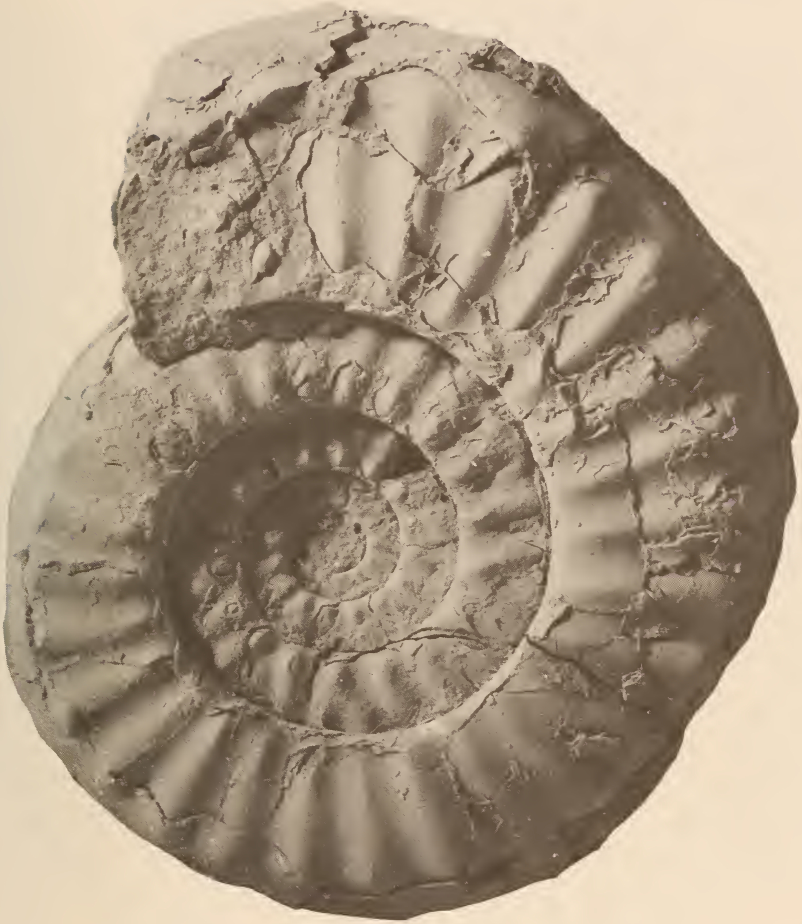

Fig. 41. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895. SAS Z1674, specimen with narrower umbilical width transitional to subgenus *P. (Zuluiceras)*. × 0,75.

P. (Z.) aberlei (Redtenbacher, 1873), *P. (Z.) isamberti* (Fallot, 1885)) to Upper Coniacian species that are much more involute and lose ornament when adult. There is no morphological break between the members of the series, and the separation proposed by Van Hoepen is considered unnecessary.

Sornayceras Matsumoto, 1965, is a further, junior synonym of *P. (Zuluiceras)*. The type species, *Sornayceras proteus* Matsumoto, 1965, is evolute and coarsely ribbed, the ribs persisting, suggesting that it is an early member of the lineage. Matsumoto (1965: 227) also mentioned that *P. undulatocarinatum* van Hoepen, 1955, here regarded as a good example of *P. (Zuluiceras)*, was a *Sornayceras*, which supports the present conclusions.

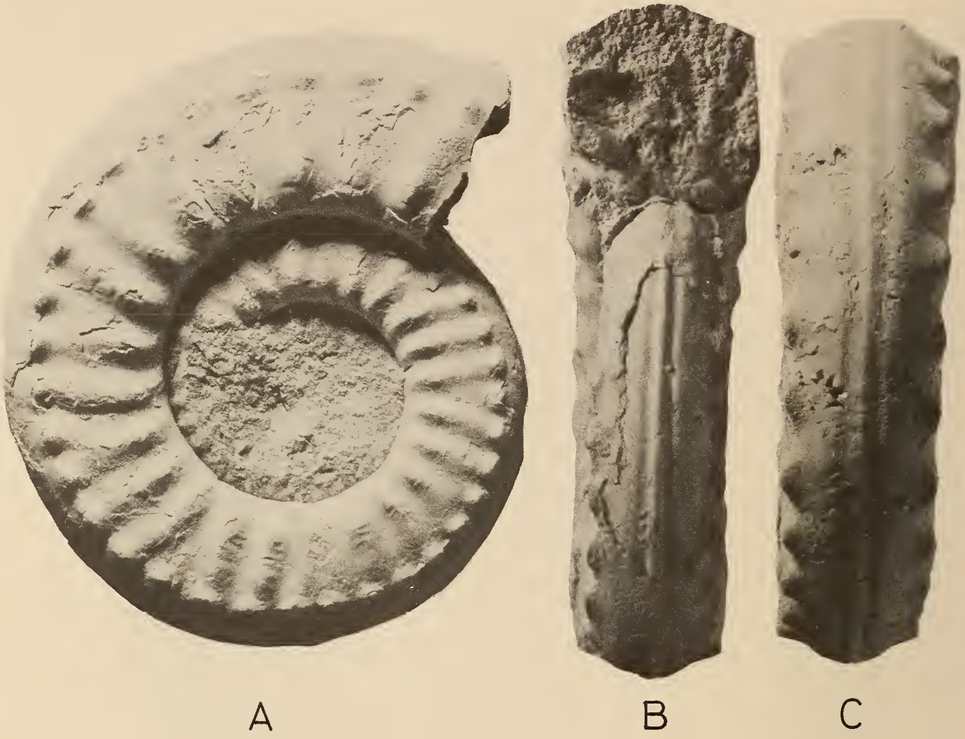

Fig. 42. *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895.
A. SAS Z1521. B–C. SAS Z1521c. All × 1.

P. (Zuluiceras) most closely resembles *P. (Peroniceras)* amongst the Peroniceratinae. The more involute coiling, compression, lateral keels subsidiary to the siphonal, and loss or weakening of ornament at maturity distinguishes them.

Occurrence

Middle Coniacian of Touraine, Aquitaine, Dieulefit (Drôme), the Corbières (Aude), Var, and Provence in France, Germany, Czechoslovakia, Austria, Italy, Romania, Armenia, north Africa, Zululand, Madagascar, and Japan. Upper Coniacian of Zululand and, possibly, Japan.

Peroniceras (Zuluiceras) zulu van Hoepen, 1965

Figs 43–52

Peroniceras sp. α Crick, 1907: 226, text-fig. to p. 226.
Peroniceras sp. ß Crick, 1907: 227.
Peroniceras (Zuluiceras) zulu van Hoepen, 1965: 9, pl. 5, text-figs 1 g–i, 2b.
Peroniceras (Zuluiceras) charliei van Hoepen, 1965: 11, pl. 6, text-fig. 1j.
Peroniceras (Zuluiceras) regularis van Hoepen, 1965: 14, pl. 9, text-fig. 3d–e.
Peroniceras (Zuluiceras) multilineatum van Hoepen, 1965: 23, pl. 18, text-fig. 5d–e.

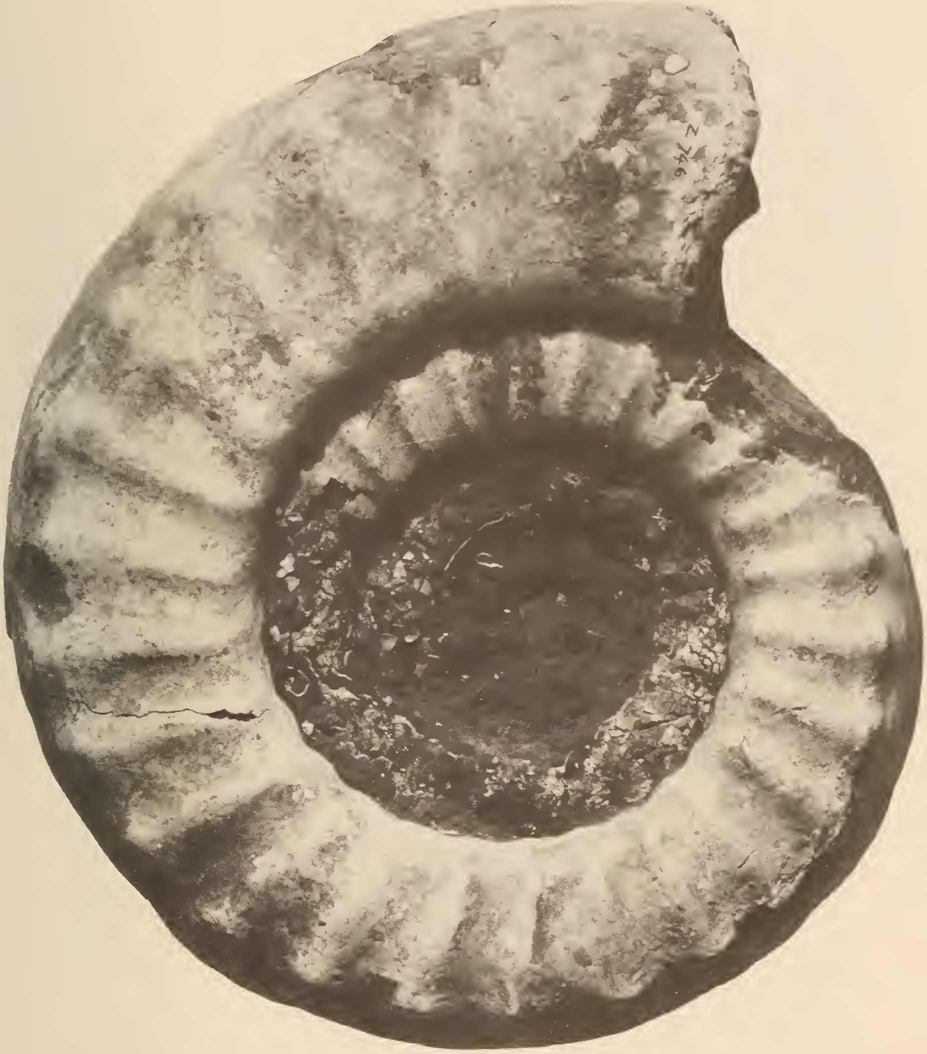

Fig. 43. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z746, the holotype. × 0.46.

Type specimen

The holotype, by original designation, is SAS Z746 (Figs 43–44), from locality 91, degraded river cliffs and artificial cut west of the boundary of the St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand. This area is strewn with rubble derived from the St. Lucia Formation, Coniacian IV and V, and the precise age of the holotype is thus unknown.

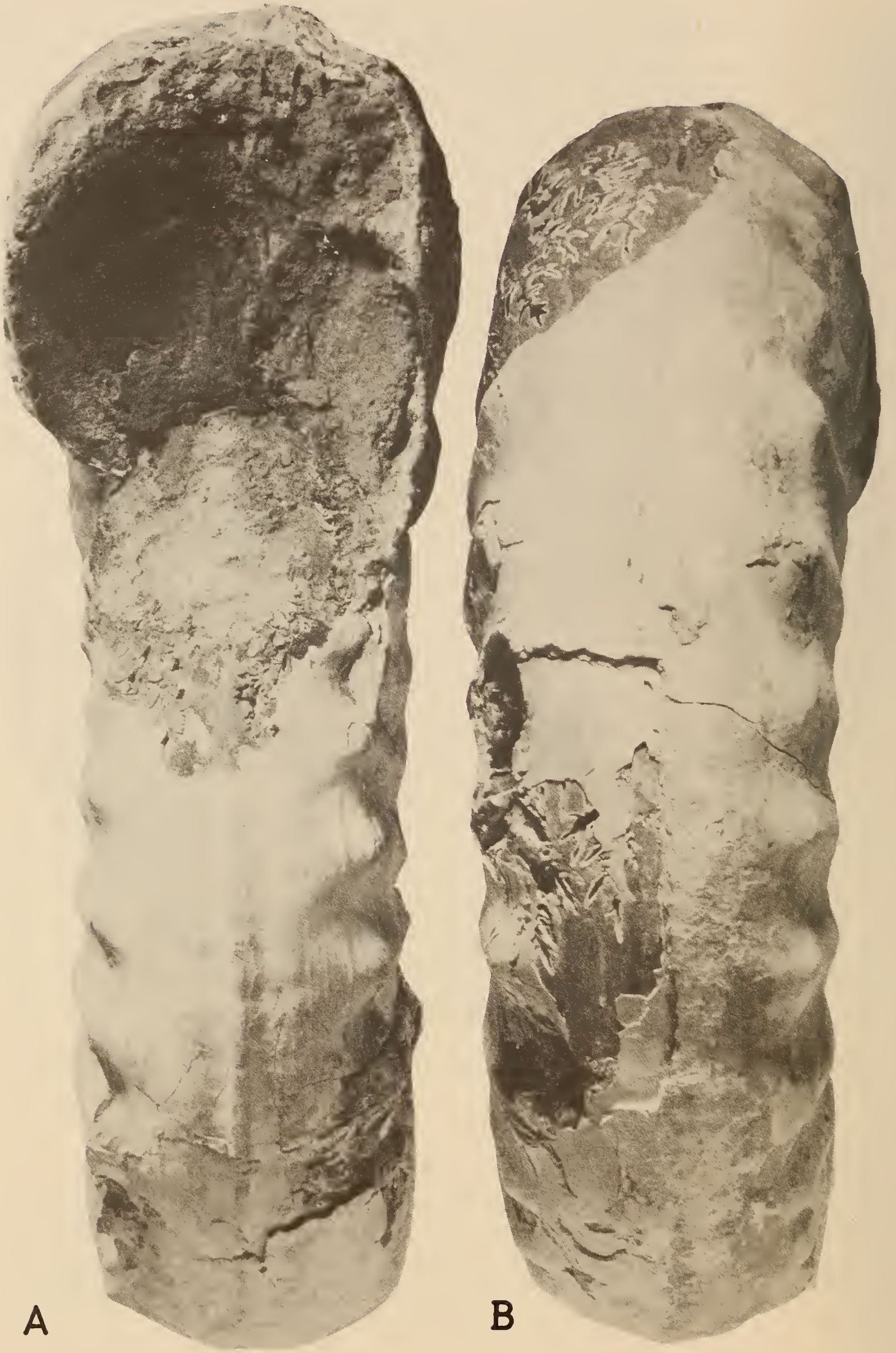

Fig. 44. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z746, the holotype. × 0,62.

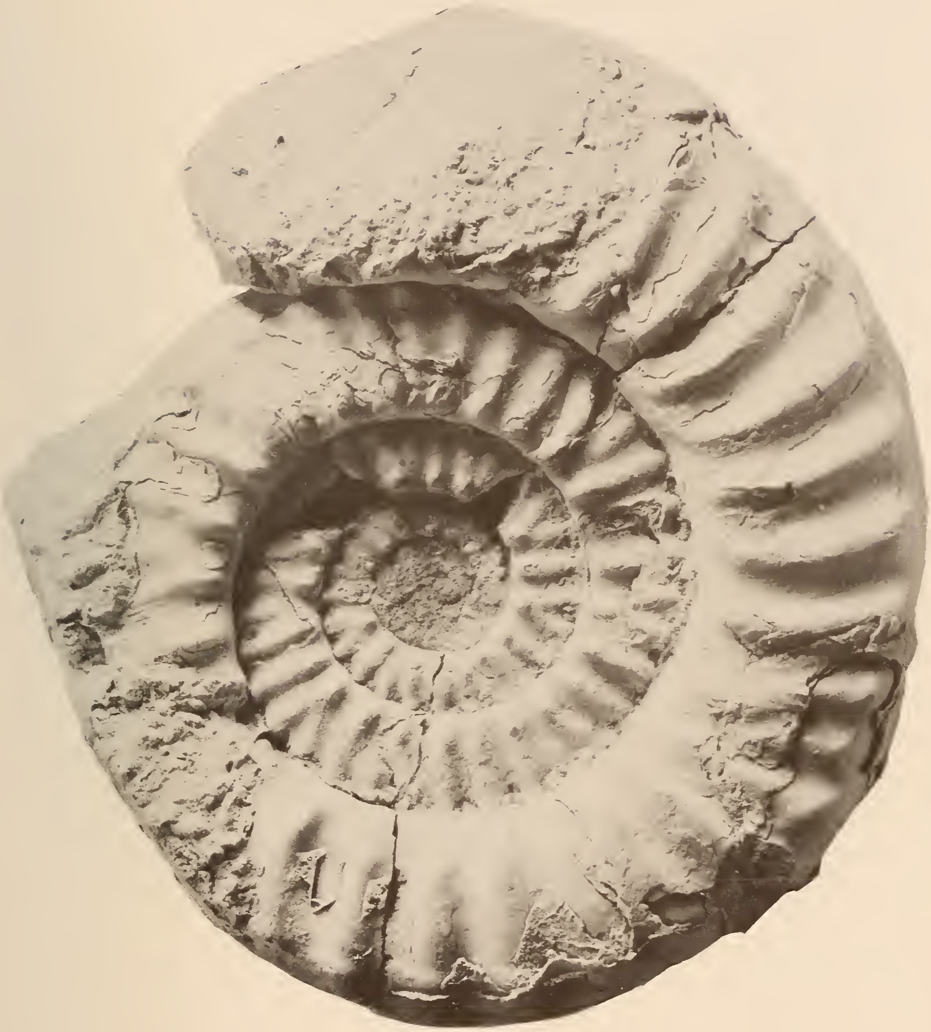

Fig. 45. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z14, one of Van Hoepen's paratypes, still close to *P. (P.) dravidicum*. × 0,8.

The type specimens of Van Hoepen's *P. (Z.) charliei, P. (Z.) regularis*, and *P. (Z.) multilineatum*, SAS Z735, Z736, and Z758 respectively, are all from the same locality as the holotype of *P. (Z.) zulu*. Their precise age is thus uncertain.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z735	110,0	39,0(35,5)	38,0(34,5)	1,03	53,0(48,2)	—
Z736	141,0	55,0(39,0)	44,0(31,2)	1,25	68,0(48,2)	22:23
Z758	158,0	52,0(32,9)	47,0(29.7)	1,10	74,0(46.8)	23:23
Z746	296,0	87,0(29,4)	92,0(31.1)	0,94	146,0(49.3)	25:25

Description

Coiling is polygyral, evolute with an umbilical diameter of 47 to 50 per cent of the total diameter. Successive whorls overlap to the ventrolateral row of tubercles.

The whorl section varies from slightly compressed to slightly depressed with a rounded to overhanging umbilical wall, slightly converging flanks and a broadly fastigiate venter with a distinct median keel (which may be serrated) as well as weaker lateral keels. The latter may disappear completely in adults.

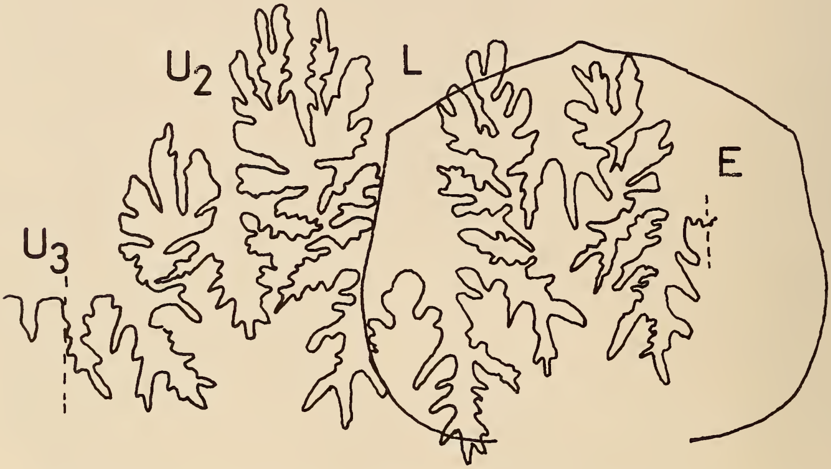

Fig. 46. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. Suture line and whorl section of holotype. × 1. (After Van Hoepen 1965, figs 1g, 2b.)

Ornament consists of rounded to radially elongated umbilical tubercles connected by ribs of varying strength to clavate ventrolateral tubercles. On the inner whorls the ribs may bifurcate or intercalate occasionally. On the outer whorls they are generally single, stronger and more distantly spaced than on nuclei. The ventral area between the row of ventral tubercles and the median keel is often ornamented by faint spiral striae. Where preservation is good, spiral ornament may also be observed on the flanks.

The suture is highly incised and of the *P. (P.) dravidicum* type (Fig. 46). The maximum body chamber length observed is half a whorl.

Discussion

This species appears to include the two specimens described by Crick (1907: 226–228) as *Peroniceras* spp. α and ß, here refigured as Figures 51–52. Van Hoepen's choice of the holotype is unfortunate as this is a large, septate

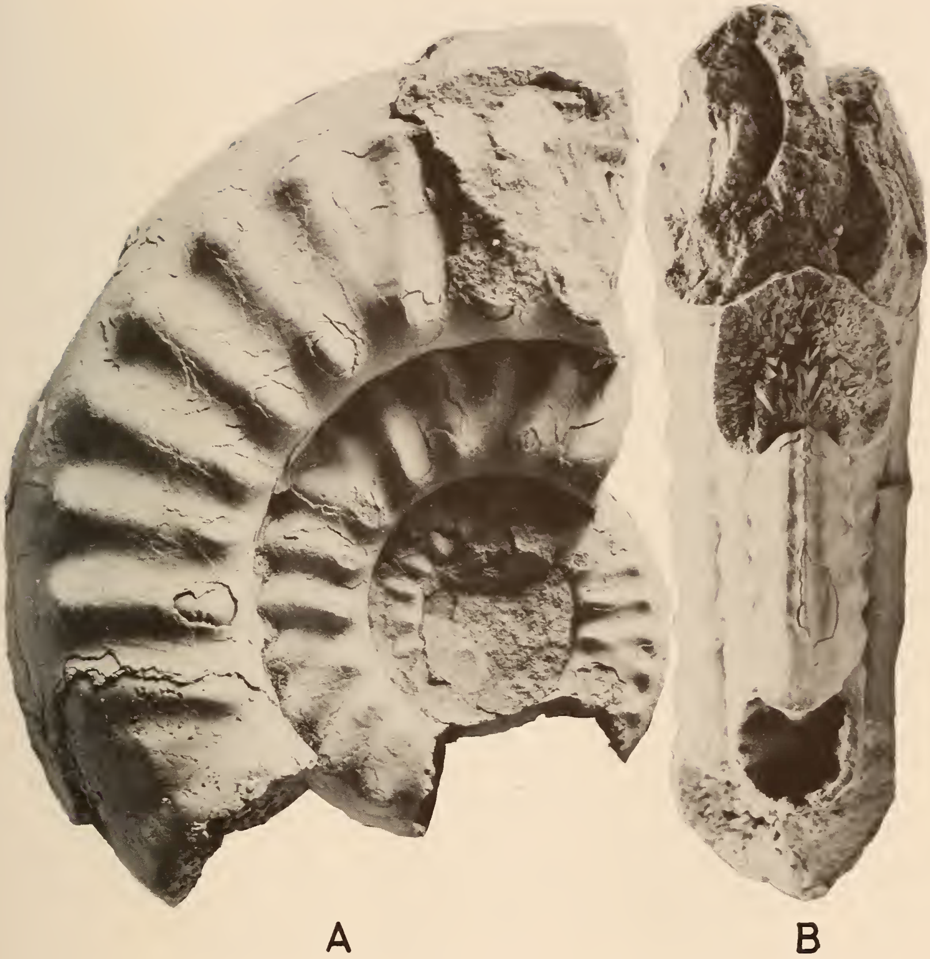

Fig. 47. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z735, the holotype of Van Hoepen's *P. (Z.) charliei*. × 1.

specimen lacking the inner whorls (Figs 43–44) and thus difficult to compare with the other material. However, as interpreted here, *P. (Z.) zulu* is an evolute form with an umbilical diameter between 45 and 50 per cent of the total diameter with whorls more or less as wide as high.

One of Van Hoepen's syntypes, SAS Z14 (Fig. 45) differs from the typical form of the species in having a more rectangular whorl section and more distinct lateral keels, and probably being in those respects transitional to *Peroniceras (Peroniceras)* of the *dravidicum* group.

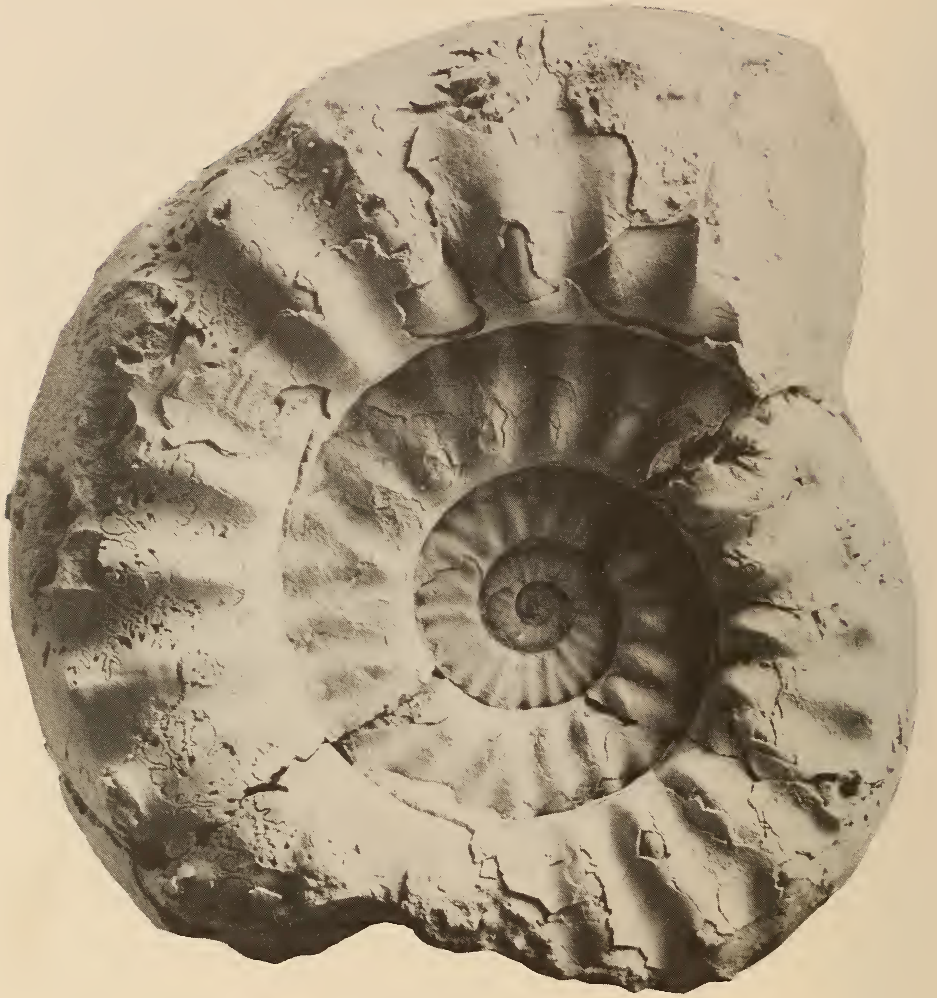

Fig. 48. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z736, the holotype of Van Hoepen's *P. (Z.) regularis.* × 0,92.

P. (Z.) zulu includes *P. (Z.) charliei* (Fig. 47), *P. (Z.) regularis* (Fig. 48), and *P. (Z.) multilineatum* (Figs 49–50), all of which are from the same locality as the holotype and have comparable proportions and ornament: the differences cited by Van Hoepen are trivial and within the range of intraspecific variation shown by other peroniceratids.

P. (Z.) zulu differs from *P. (Z.) henniei* in having a wider umbilicus and more angular whorl section, but it is clear that the latter is derived from *P. (Z.) zulu* through progressive increase in involution and rounding of the whorl section. In addition, there is a reduction of the lateral keels and progressive serration of the median keel.

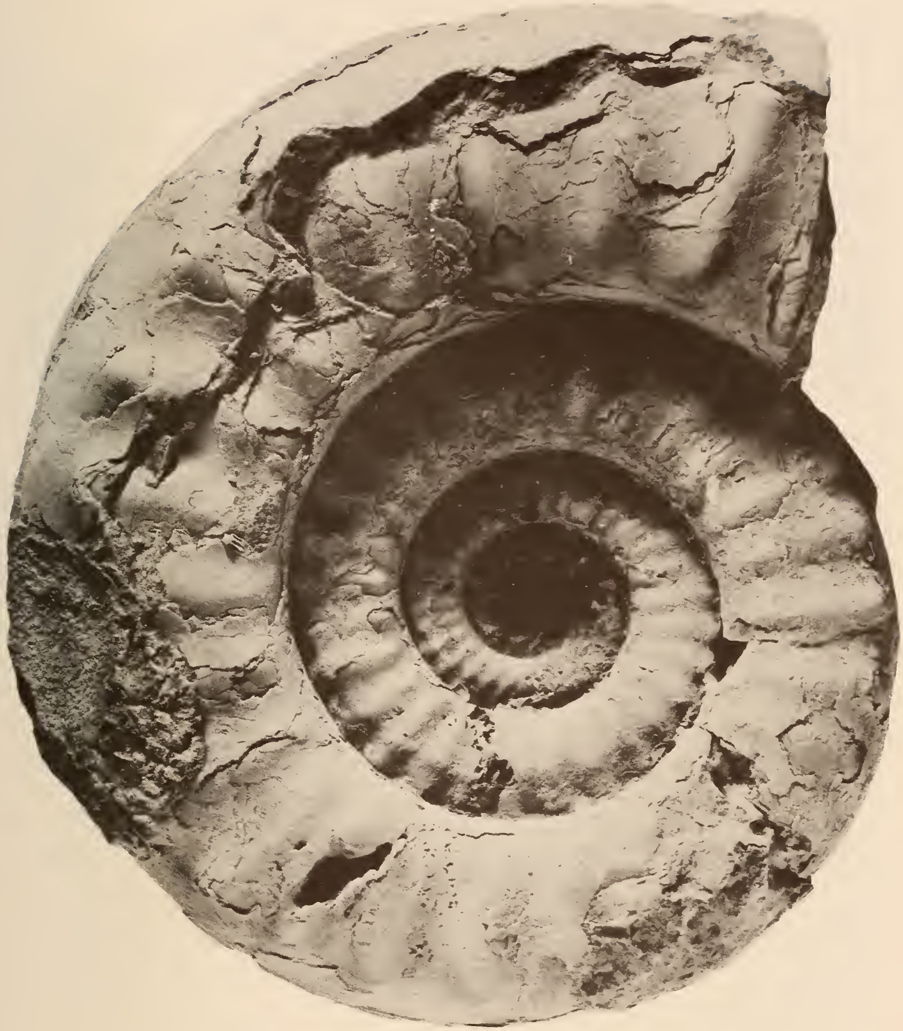

Fig. 48. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z736, the holotype of Van Hoepen's *P. (Z.) regularis.* × 0,92.

In *P. (P.) dravidicum* the whorl section is more rectangular and the coiling more evolute.

Occurrence

The horizon of the type material is difficult to establish as the specimens were collected loose. Material collected *in situ* is restricted to Coniacian IV, which is presumed to be the level of the type specimens. The species is restricted to Zululand.

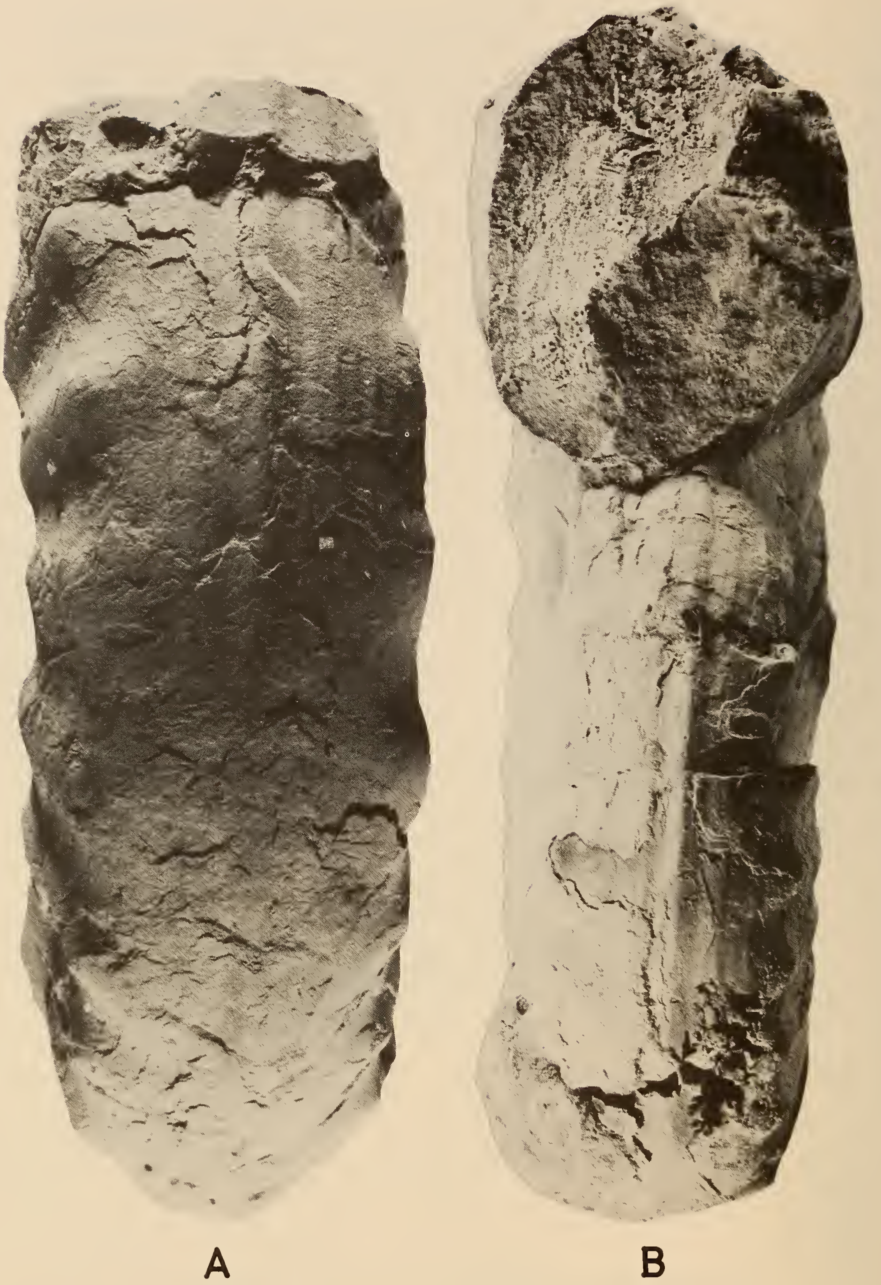

Fig. 50. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. SAS Z758, the holotype of Van Hoepen's *P. (Z.) multilineatum*. × 0,8.

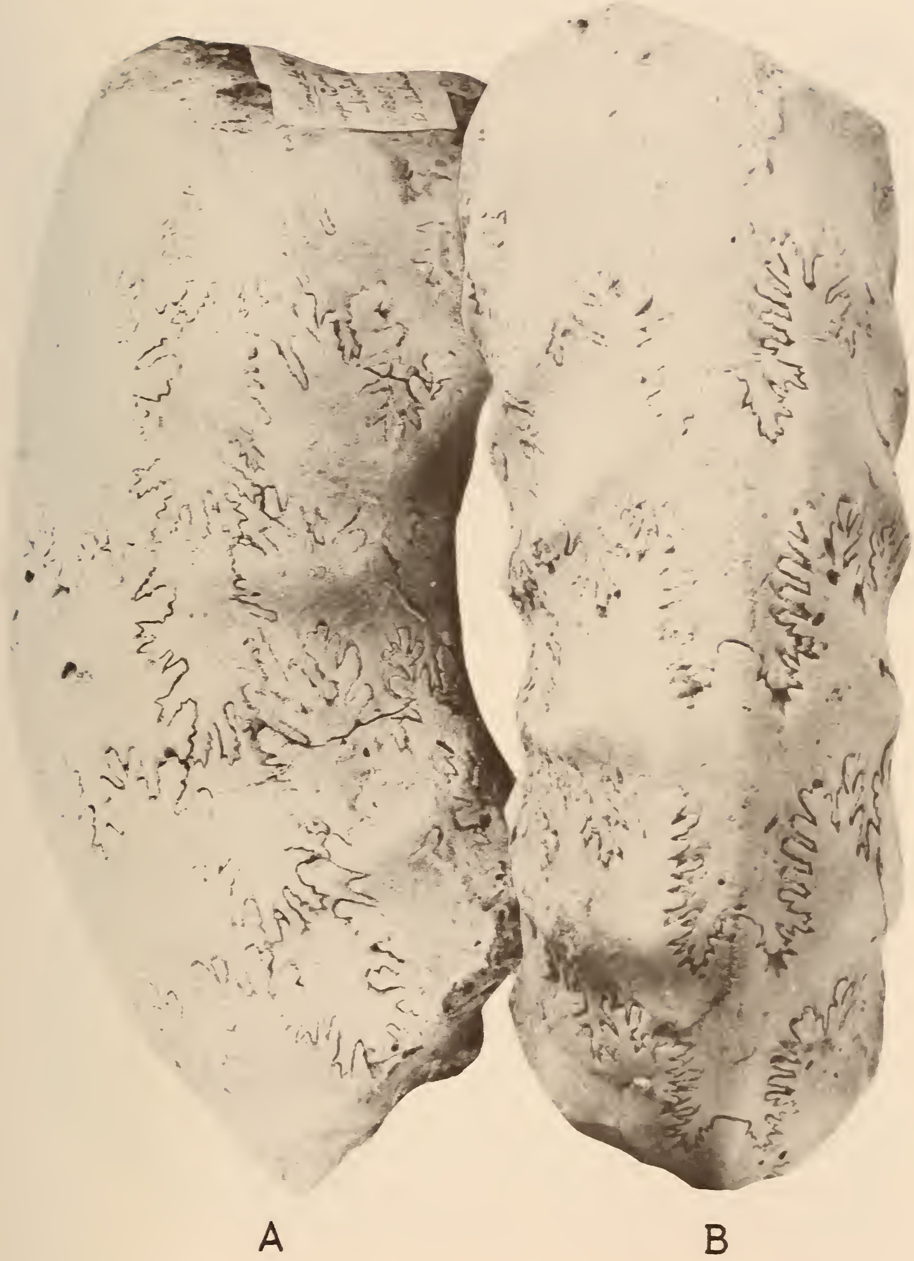

Fig. 51. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. The original of Crick's (1907)*Peroniceras* sp. α. × 0.85.

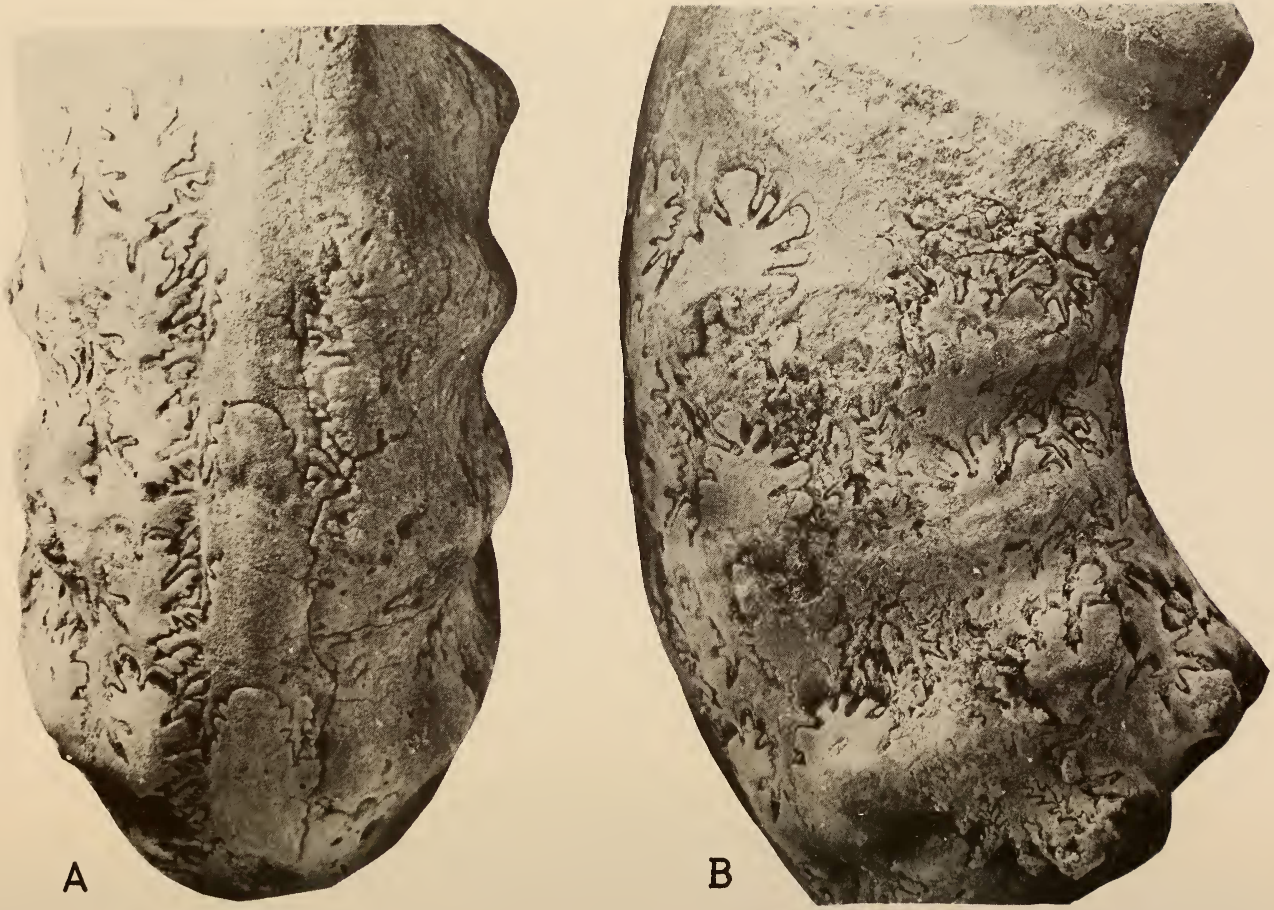

Fig. 52. *Peroniceras (Zuluiceras) zulu* van Hoepen, 1965. The original of Crick's (1907) *Peroniceras* sp. ß. × 1.

Peroniceras (Zuluiceras) rarum van Hoepen, 1965

Fig. 53

Peroniceras (Zuluiceras) rarum van Hoepen, 1965: 16, pl. 12, text-fig. 4(c).

Type specimen

Holotype, by monotypy, is SAS Z742 from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV or V, probably the former.

Material

BMNH C83865, from locality 83, foreshore exposures around Mason's Camp, western shores of False Bay, east-north-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z742	100,0	32,0(32,0)	36,0(36,0)	0,89	38,0(38,0)	—

Description

The holotype consists of part of a septate, crushed whorl. Coiling is rather involute with an umbilical diameter of 38 per cent. The whorl section throughout is compressed with little inflated, parallel flanks and a gently rounded, fastigiate venter bearing a distinct crenulate central keel and poorly defined lateral keels.

Lateral ornament consists of weak umbilical bullae, narrow, rectiradiate, occasionally bifurcating ribs, and rounded to clavate ventrolateral tubercles. Faint traces of spiral ornament are visible in the area between the ventrolateral tubercles and the faint lateral keels.

The suture is only partially exposed, but appears to be of the general *P. (P.) dravidicum* type.

Discussion

It is regrettable that Van Hoepen erected a new species on such incomplete material, which renders interpretation difficult. As far as the whorl section is concerned, the species is allied to the group of *P. (P.) dravidicum*, but the crenulate keel and more involute coiling places it closer to the group of *P. (Zuluiceras)*. It differs from *P. (Z.) zulu* by the tighter coiling. The more tightly coiled group of *P. (Z.) henniei* differs from *P. (Z.) rarum* in having a more inflated whorl section at comparable diameters.

Lacking more material for additional observations, the species is here maintained with doubt.

Occurrence

The type locality includes rubble derived from Kennedy & Klinger's (1975) divisions Coniacian IV and V, so that the precise age is unknown. The second specimen is firmly dated as Coniacian IV. The species is known only from Zululand.

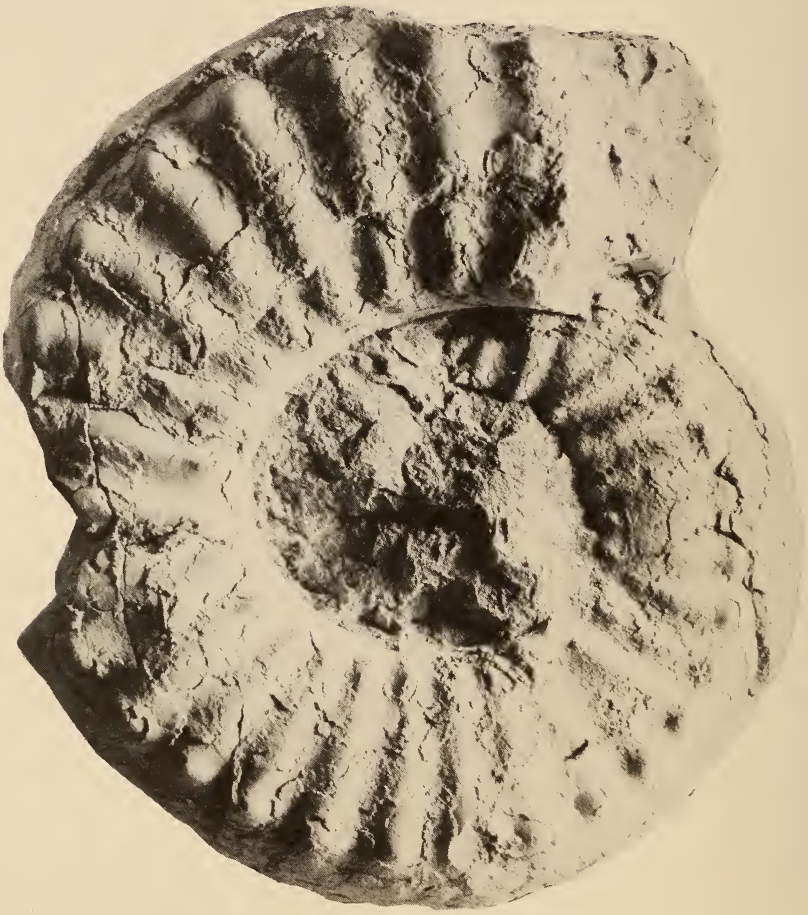

Fig. 53. *Peroniceras (Zuluiceras) rarum* van Hoepen, 1965.
SAS Z742, the holotype. × 1.

Peroniceras (Zuluiceras) henniei van Hoepen, 1965

Figs 54–64

Peroniceras (Zuluiceras) henniei van Hoepen, 1965: 12, pl. 7, text-fig. 1k.
Peroniceras (Zuluiceras) alfredmeintjesi van Hoepen, 1965: 15, pl. 10, text-fig. 3b–c.
Peroniceras (Zuluiceras) simplicicostatum van Hoepen, 1965: 16, pl. 11, text-fig. 3a, g.
Peroniceras (Zuluiceras) undulatocostatum van Hoepen, 1965: 19, pl. 14, text-fig. 4a–b.
? Peroniceras (Zuluiceras) similis van Hoepen, 1965: 19, pl. 15, text-figs 2a, 4d.
Peroniceras (Zuluiceras) proximum van Hoepen, 1965: 20, pl. 16 text-fig. 5a–b.
Peroniceras (Zuluiceras) ultimum van Hoepen, 1965: 22, pl. 17, text-fig. 5c.

Type specimens

The holotype, by original designation, is SAS Z638 from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV or V. The type specimens of *P. (Z.) alfredmeintjesi*, SAS Z738, *P. (Z.) simplicicostatum*, SAS Z740, *P. (Z.) proximum*, SAS Z747, *P. (Z.) ultimum*, SAS Z752, *P. (Z.) undulatocostatum*, SAS Z744, *P. (Z.) similis*, SAS Z745 and SAS 104, are all from the same locality as the holotype, and are equally imprecisely dated.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z638	115,0	41,0(35,6)	42,0(35,6)	0,98	46,0(40,0)	12×12:12×2
Z752	130,0	46,0(35,4)	44,0(33,8)	1,04	56,0(43,1)	21:34
Z738	150,0	54,0(36,0)	53.0(35,3)	1,02	64,0(42,7)	26:31
Z745	178,0	61,0(34,3)	60,0(33,7)	1,02	79.0(44,4)	—
Z747	262,0	81,0(30,9)	87,0(33,2)	0,93	115,0(43,9)	—
Z740	283,0	88,0(31,1)	97,0(34,3)	0,91	115,0(40,6)	23:25
Z744	345,0	139,0(40,3)	125,0(36,3)	1,11	140,0(40,6)	—

Description

The species has an umbilical diameter varying between 40 and 45 per cent of the total diameter. The whorls are slowly expanding, overlapping up to or beyond the ventrolateral tubercle. The whorl changes through ontogeny; it is initially quadrate with flattened flanks, but in later stages the umbilical wall becomes rounded and the flanks inflated. The venter is broadly rounded with a serrated central keel and weak lateral keels.

The adult whorl section varies among specimens as discussed below.

Ornament on the inner whorls is of *P. (P.) dravidicum* type, with umbilical bullae giving rise to one or two ribs that link ventrolateral clavi. On the outer whorls ribbing becomes bolder, and bifurcations rather rare. The ventral area between the ventrolateral tubercles and the central keel is ornamented by fine, spiral, interrupted striae. The undulations on the keel are far more numerous than the ventrolateral clavi.

The suture-line is of the *P. (P.) dravidicum* type (Fig. 61).

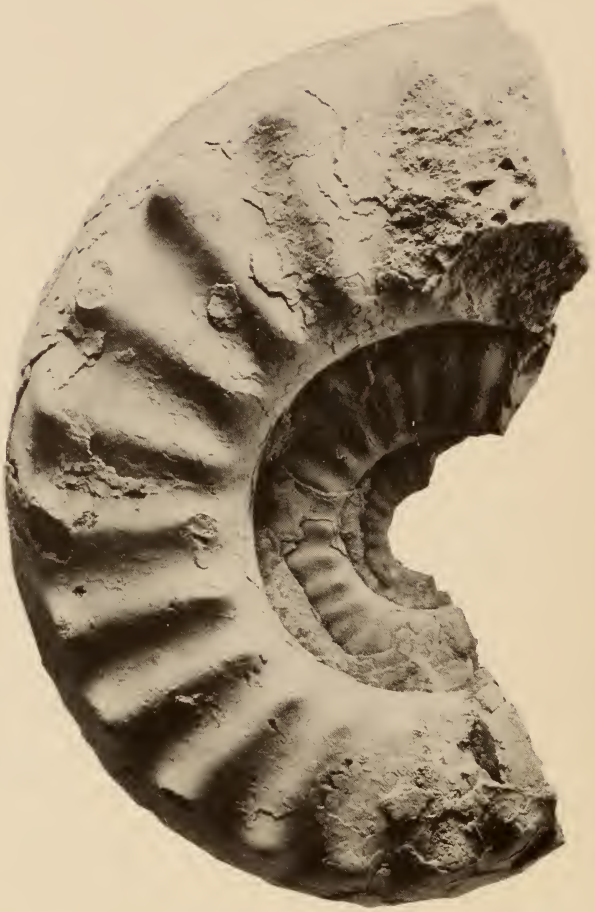

Fig. 54. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965.
SAS Z638, the holotype. × 1.

Discussion

The authors' interpretation of the species is somewhat different from that of Van Hoepen (1965) and includes all forms with an umbilical diameter of between 40 and 45 per cent, more or less equal whorl breadth and height, serrated central keel, and very weak or no lateral keels. This species continues the morphological trend set by *P. (Z.) zulu* towards tighter coiling and loss of ornament on the outer whorls.

The description given above covers a number of species described by Van Hoepen, all collected from the same locality. These species (listed in the synonomy) take the name *P. (Z.) henniei.*

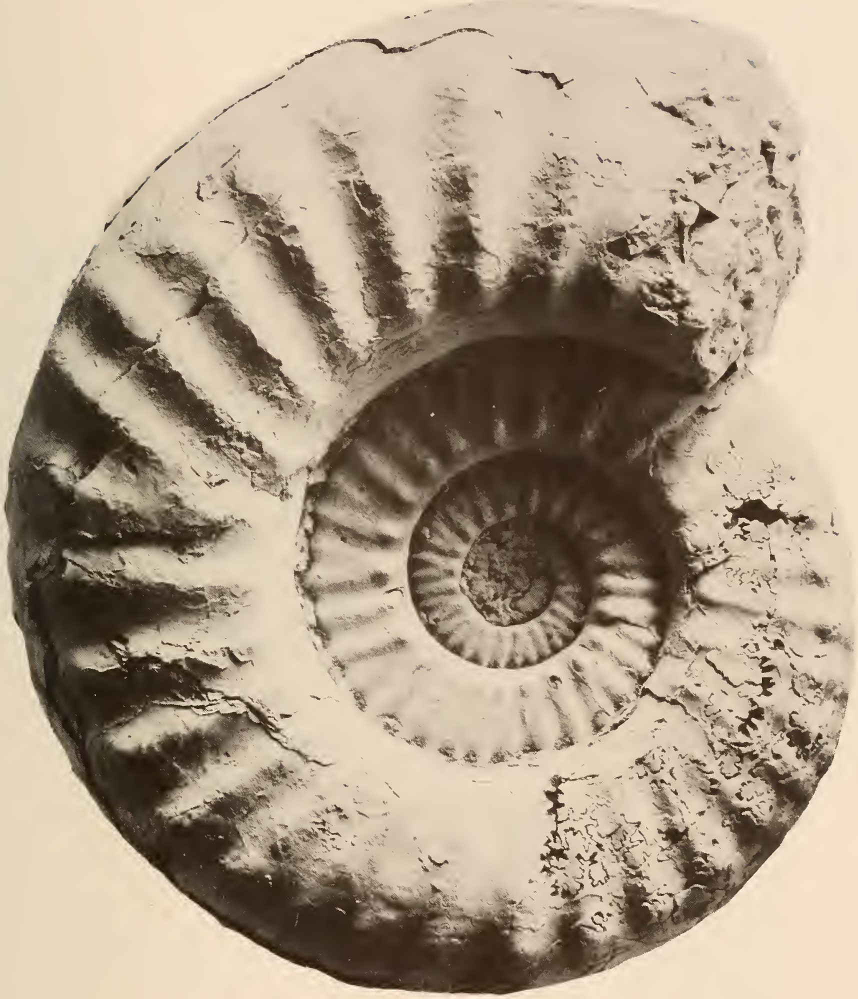

Fig. 55. *Peroniceras (Zuluiceras) henniei* van Hoepen. This specimen and that in Figure 57 show the features of the species to the best advantage. × 0,8.

The holotype of *P. (Z.) henniei* (Fig. 54) consists of parts of three consecutive whorls, of which the last quarter of the outermost one is body chamber. The impression of an earlier whorl shows that the venter is already unicarinate and serrated at a diameter of 12,5 mm. As far as the angular whorl section is concerned, this specimen is perhaps closest to *P. (Z.) zulu.*

The holotype of *P. (Z.) alfredmeintjesi* (Figs 55–56A) is the best preserved of all the specimens and shows the main features of the species. The inner whorls are typically quadrate, whereas the outer whorls are more rounded. A

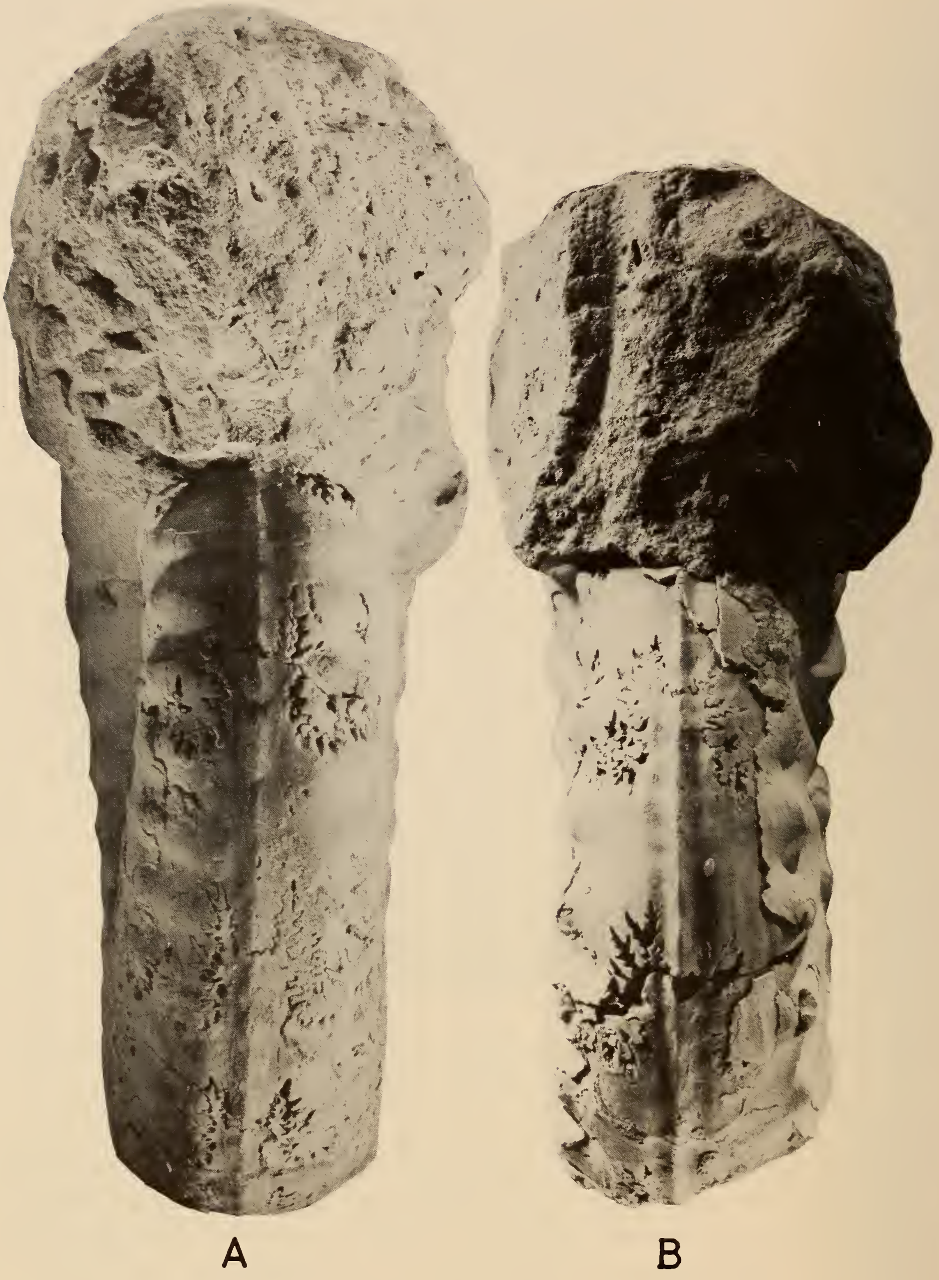

Fig. 56. A. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z738, the holotype of Van Hoepen's *P. (Z.) alfredmeintjesi*. × 0,9. B. *Peroniceras (Zuluiceras) zulu* van Hoepen. × 0,88.

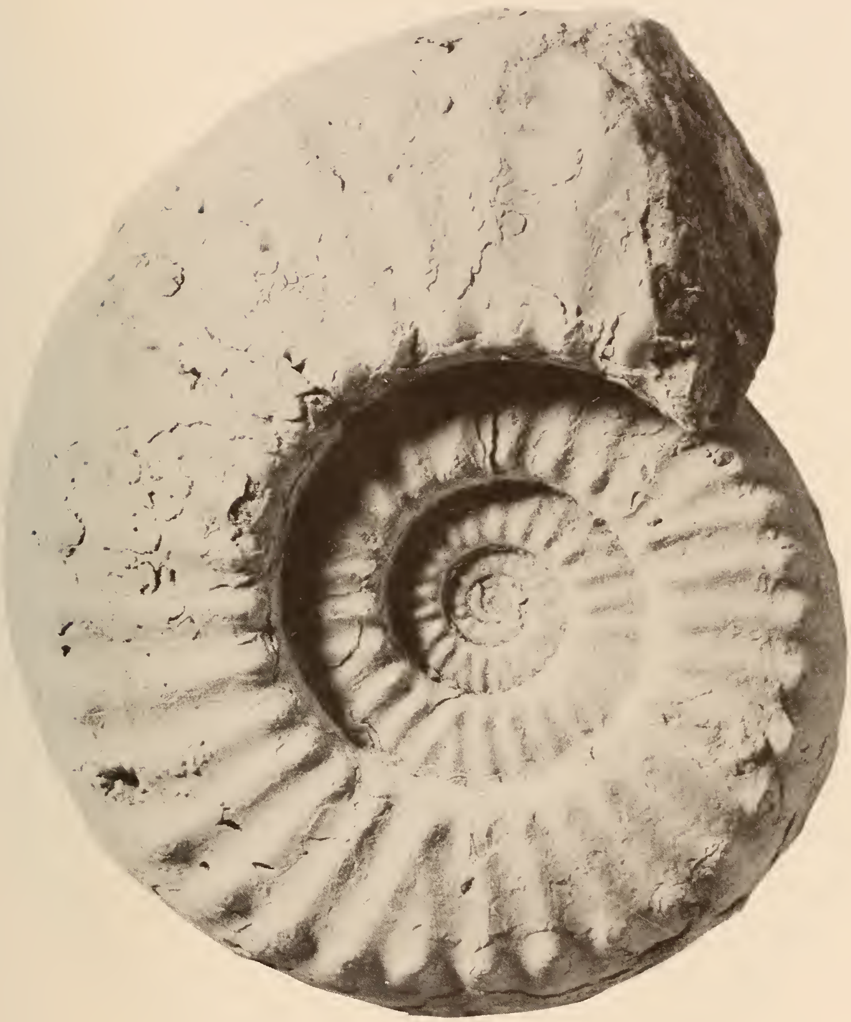

Fig. 57. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS A374. × 1.

nodate *Baculites*, presumably of the group *B. capensis* Woods, is present in the body chamber of this specimen.

The holotype of *P. (Z.) simplicicostatum* (Figs 58–59) is an enormous individual, still septate at a diameter of 306 mm. Unfortunately the inner whorls up to a diameter of 90 mm are not preserved. The whorls are much more massive and increase in size is more rapid than in the preceding specimens. Also, whorl height exceeds whorl breadth considerably. In this respect the specimen is closer to *P. (Z.) undulatocarinatum* described below, but has a slightly greater umbilical width than the latter species. The specimen figured by De Grossouvre (1894,

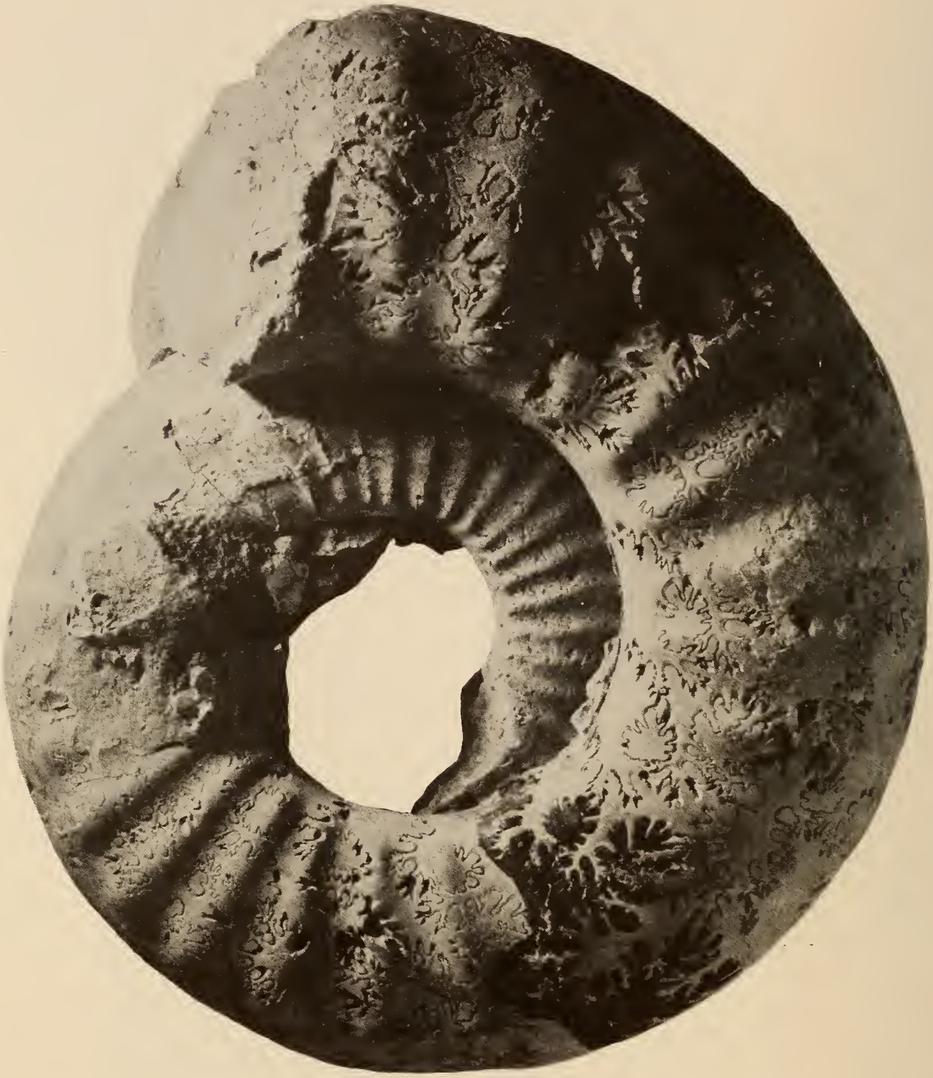

Fig. 58. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z740, the holotype of *P. (Z.) simplicicostatum* van Hoepen. × 0,47.

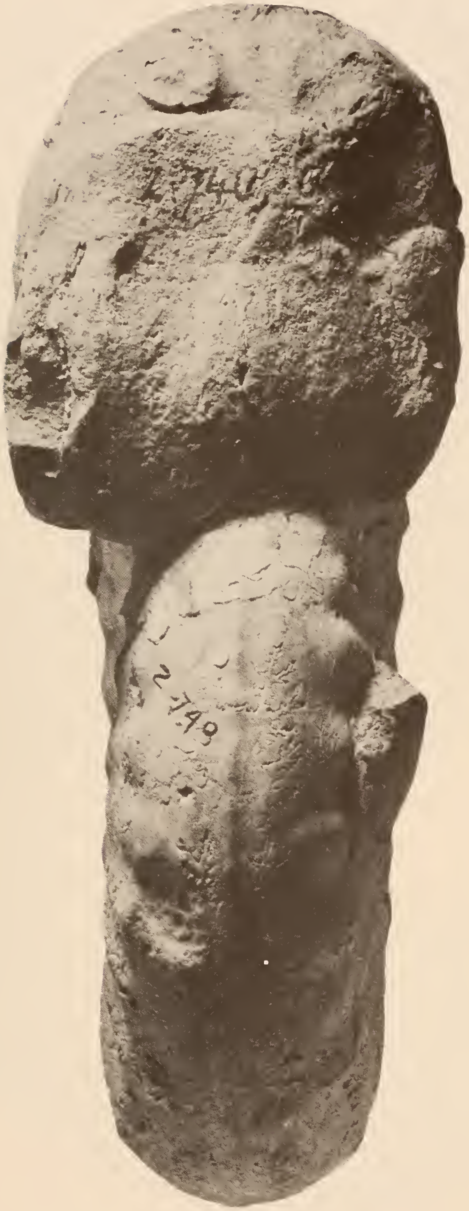

Fig. 59. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z740, the holotype of *P. (Z.) simplicicostatum* van Hoepen, 1965. × 0,53.

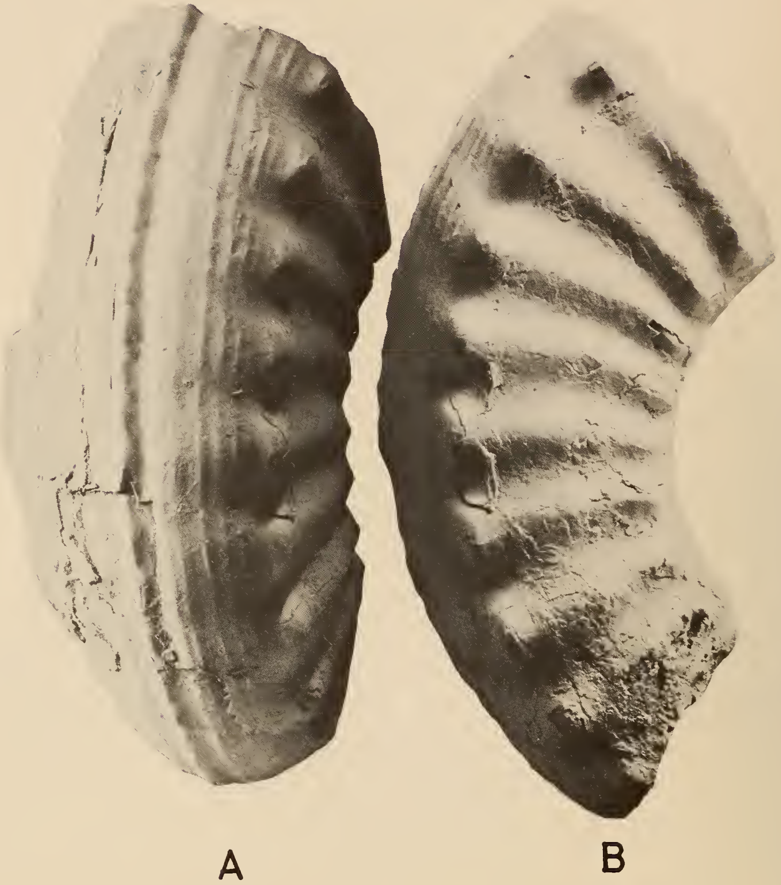

Fig. 60. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z744, inner whorls of the holotype of *P. (Z.) undulatocostatum* van Hoepen, 1965. × 1.

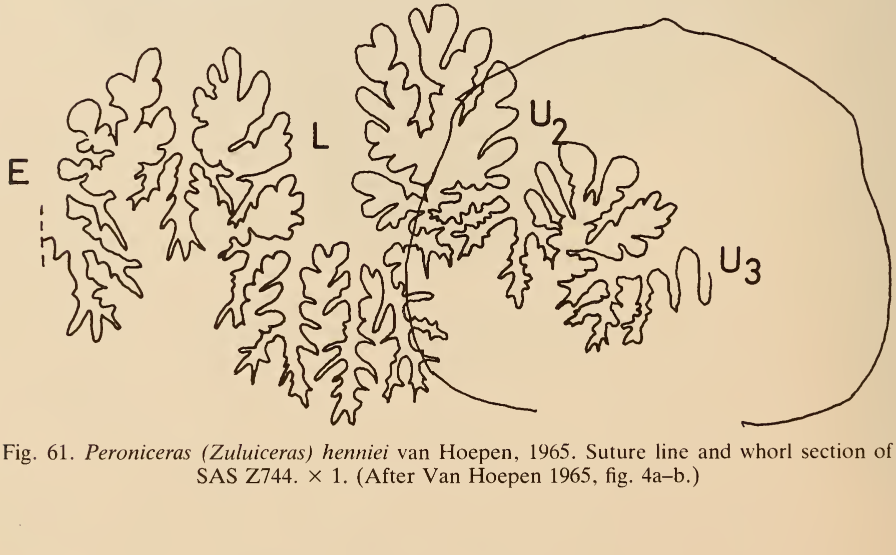

Fig. 61. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. Suture line and whorl section of SAS Z744. × 1. (After Van Hoepen 1965, fig. 4a–b.)

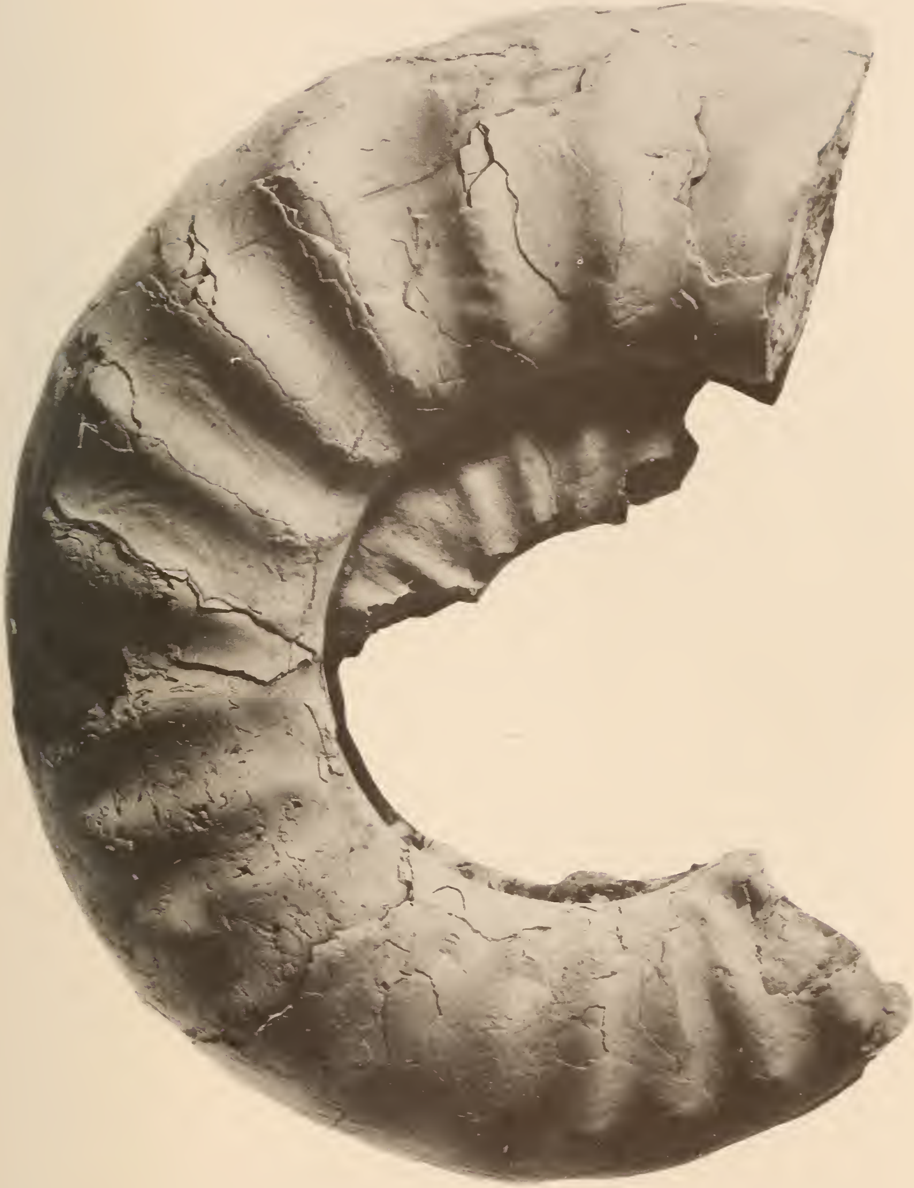

Fig. 62. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z747, the holotype of *P. (Z.) proximum* van Hoepen, 1965. × 0.6.

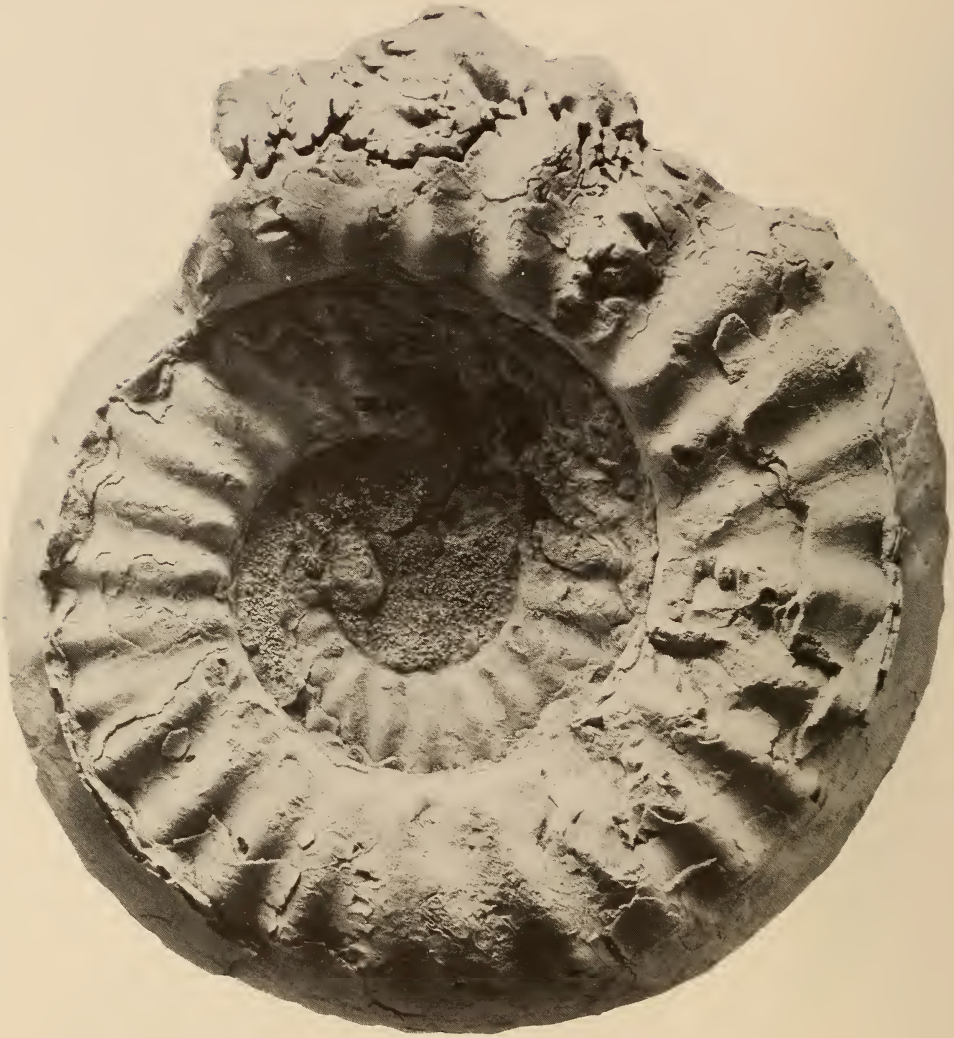

Fig. 63. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS Z752, the holotype of *P. (Z.) ultimum* van Hoepen, 1965. × 1.

pl. 9 (fig. 1)) as an adult of *Gauthiericeras bajuvaricum* is a comparable but poorly preserved European analogue.

The holotype of *P. (Z.) undulatocostatum* is another gigantic specimen with a maximum measured diameter of 533 mm. Unfortunately only part of the inner whorls survive, but Van Hoepen's figure of the holotype is adequate also to show it as a transitional form between *P. (Z.) henniei* and *P. (Z.) undulatocarinatum*. Part of the inner whorl is preserved with some of the shell still intact. This shows the finely serrated central keel and finely striate radial ornament in the ventral area between the keel and the ventrolateral tubercles (Fig. 60).

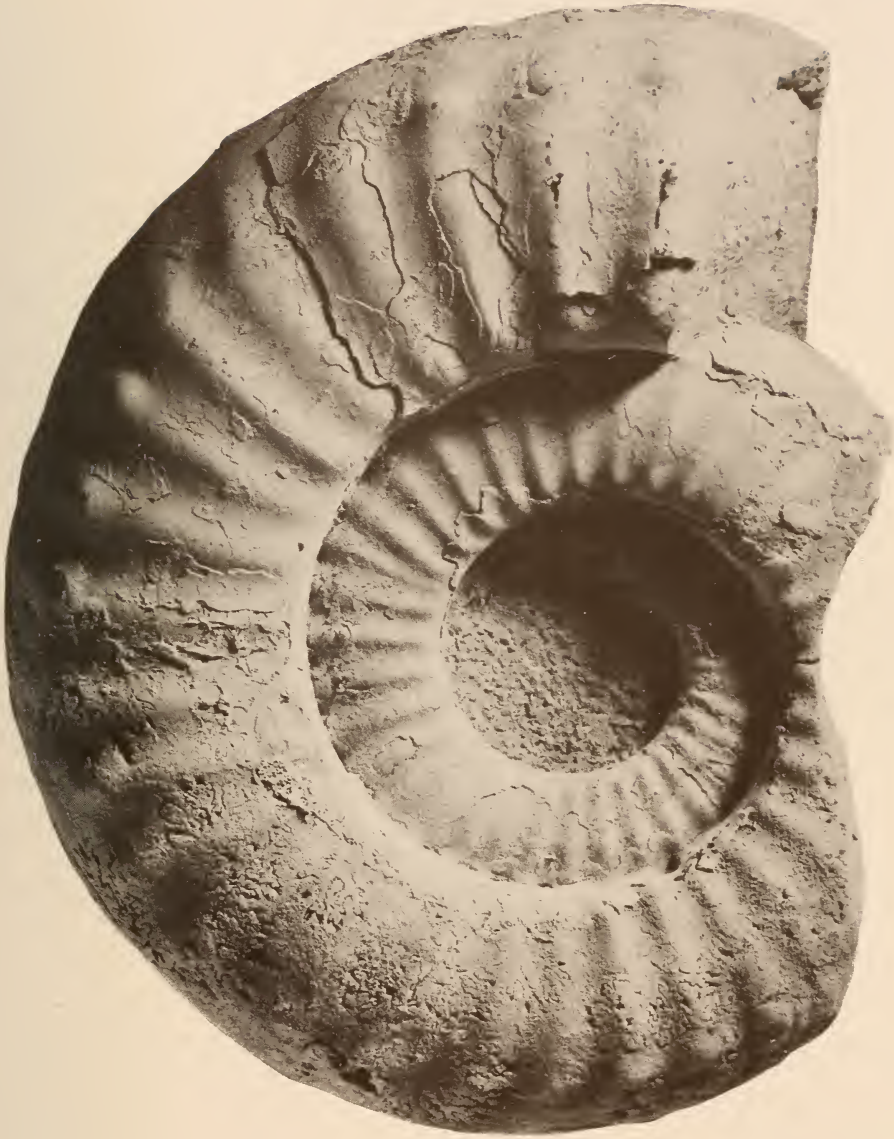

Fig. 64. *Peroniceras (Zuluiceras) henniei* van Hoepen, 1965. SAS 104, a loosely coiled specimen transitional to *P. (Z.) zulu*. × 0,73.

The holotype of *P. (Z.) similis* is not available for study, but from the descriptions and figures it seems to be a more evolute form connecting *P. (Z.) henniei* with *P. (Z.) zulu*. The holotype of *P. (Z.) proximum* (Fig. 62) is also a large specimen consisting of part of two successive whorls of which only a small part is body chamber. Again the looser coiling suggests that it connects morphologically with *P. (Z.) zulu*.

The holotype of *P. (Z.) ultimum* (Fig. 63) is a septate disc 130 mm in diameter. Apart from details of preservation, the outer whorls of this specimen are indistinguishable from the inner whorls of the holotype of *P. (Z.) undulatocostatum*, and is thus a further clear synonym of *P. (Z.) henniei*.

The species is here interpreted more widely than by Van Hoepen, but the authors doubt if the differences between the various 'species' given by that author are of specific significance. All the species are based on single specimens that occur at essentially the same stratigraphic level, which further causes one to doubt their validity. In consequence they are all here included in *P. (Z.) henniei*.

The next species to be discussed, *P. (Z.) undulatocarinatum*, continues the trend towards closer coiling, but here a progressive loss of ornament on the outer whorls spans the boundary between Van Hoepen's 'subgenera' *P. (Zuluiceras)* and *P. (Zuluites)*.

Occurrence

The type locality is strewn with rubble from Coniacian IV and V; the species is probably from the former. It may possibly also occur in France.

Peroniceras (Zuluiceras) undulatocarinatum van Hoepen, 1955

Figs 65–75

Peroniceras undulatocarinatum van Hoepen, 1955: 369, figs 18–21.
Peroniceras (Zuluites) georgemeintjesi van Hoepen, 1965: 25, pl. 20, text-fig. 6c–e.
Peroniceras (Zuluites) lettiae van Hoepen, 1965: 27, pl. 21, text-fig. 7a–d.
? Peroniceras (Zuluites) dubium van Hoepen, 1965: 28, pl. 22, text-fig. 7b–c.

Type specimens

The holotype, by original designation, is SAS Z15 (Fig. 73) from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand. This locality is strewn with rubble from the St. Lucia Formation, Coniacian IV and V, and the specimen cannot be precisely dated, although it is probably from Coniacian IV. The holotype of *P. (Zuluites) georgemeintjesi* is SAS Z733; the holotype of *P. (Z.) lettiae* is SAS Z185; the holotype of *P. (Z.) dubium* is SAS Z750. Other specimens are SAS Z19, Z631, Z742, and Z868, all from the same locality. Some specimens are associated with nodose *Baculites*, suggesting that they are from Coniacian IV.

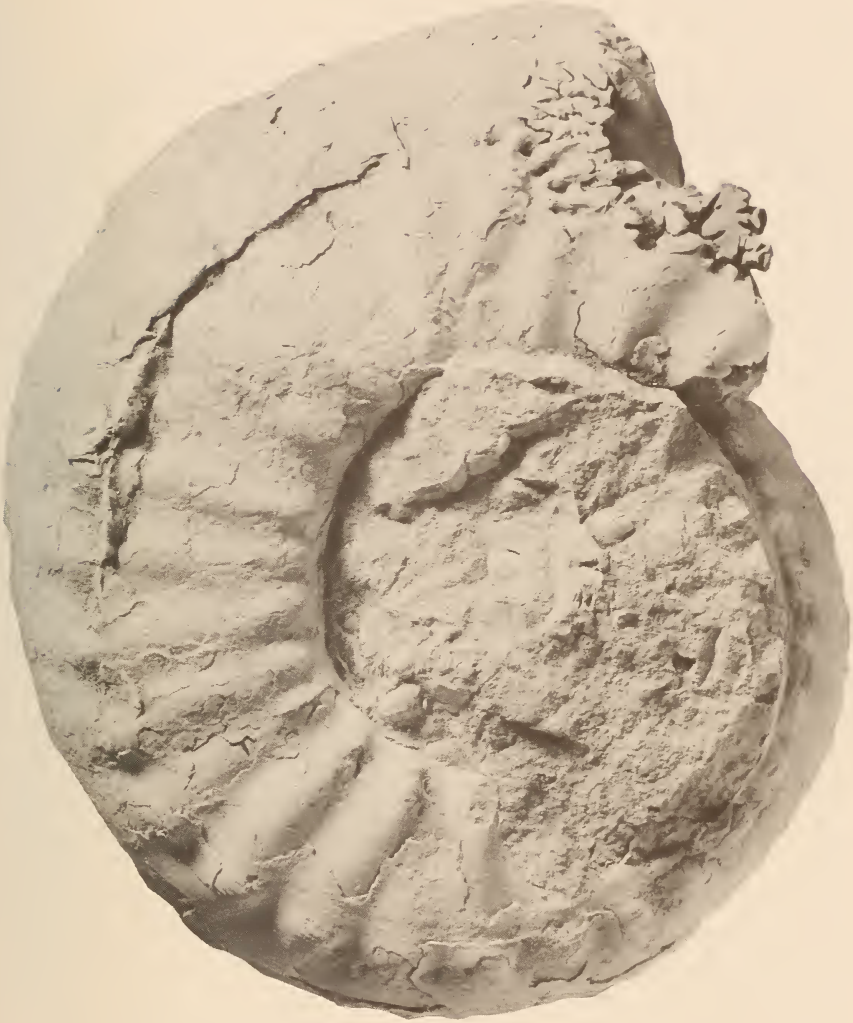

Fig. 65. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z19, inner whorls of paratype of Van Hoepen (1955). × 0,95.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z19	142,0	49,0(34,5)	55,0(38,7)	0,89	55,0(38,7)	13×2:30
Z750	148,0	42,0(28,3)	54,0(36,5)	0,78	58,0(39,2)	11×2:13×2
Z15	159,0	54,0(34,0)	59,0(37,1)	0,95	64,0(40,2)	14×2:14×2
Z733 at	154,0	48,0(31,2)	60,0(39,0)	0,80	55,0(35,7)	—
at	218,0	63,0(28,9)	87,0(39,9)	0,72	84,0(38,5)	—
Z185	174,0	62,0(35,6)	68,0(39,1)	0,91	72,0(41,4)	—

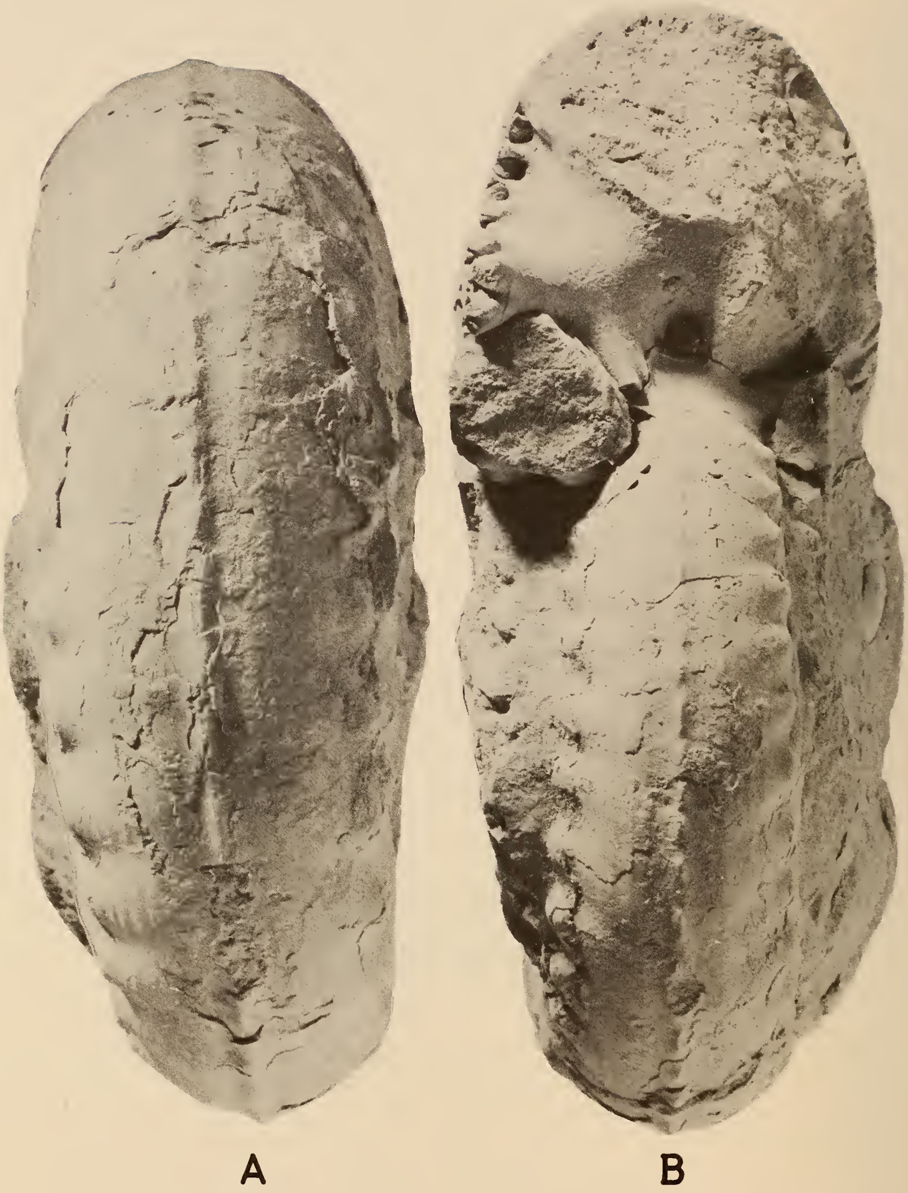

Fig. 66. A–B. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955 SAS Z19, inner whorls of paratype of Van Hoepen (1955). × 1.

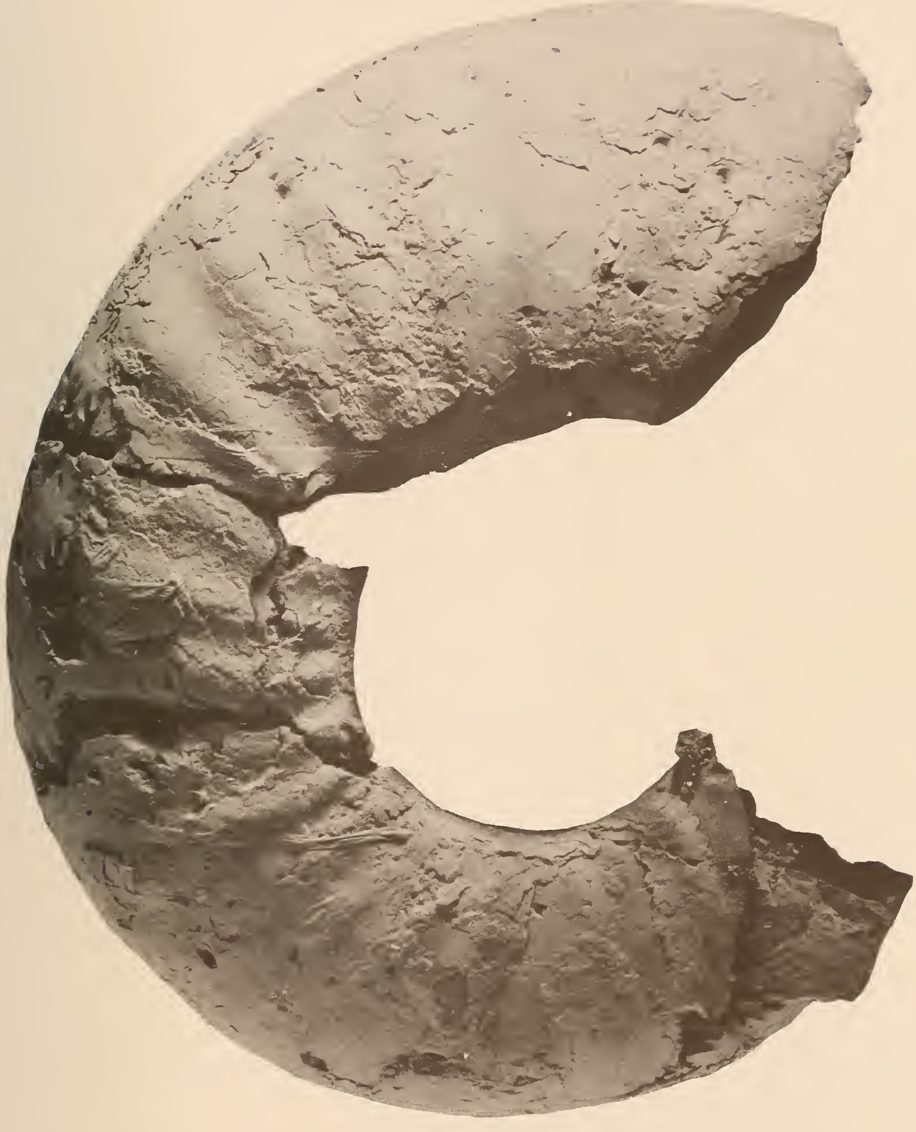

Fig. 67. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1965. SAS Z19, outer whorl of paratype of Van Hoepen (1955). × 0,75.

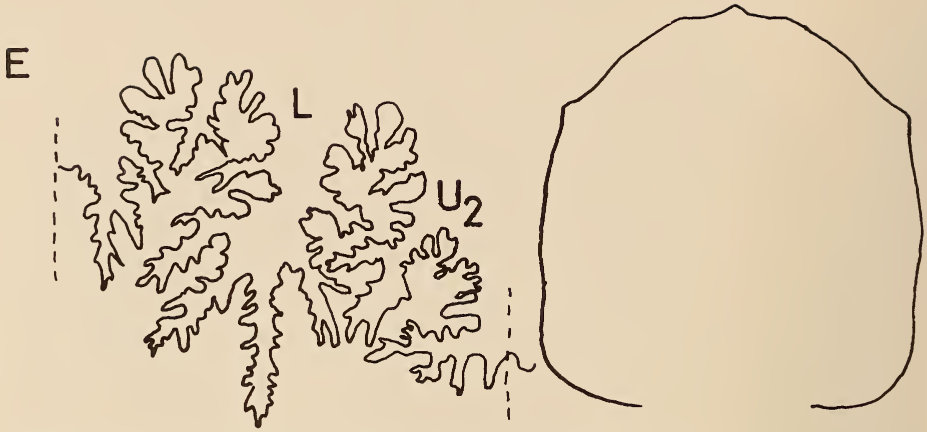

Fig. 68. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line and whorl section of the holotype, SAS Z15. × 1. (After Van Hoepen 1955, figs 19–20.)

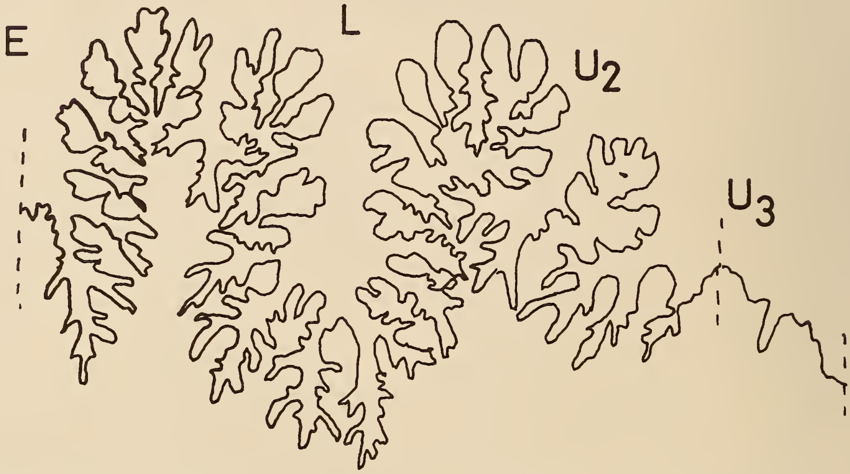

Fig. 69. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line of paratype SAS Z19. × 1. (After Van Hoepen 1955, fig. 22.)

Coiling is involute for *Peroniceras*, with an umbilical diameter of between 35 and 40 per cent of the total diameter. Successive whorls overlap up to and beyond the ventrolateral tubercles.

The whorl section is distinctly compressed, with a vertical to overhanging rounded umbilical wall, little-inflated, rounded flanks converging to a broadly rounded-fastigiate venter (Fig. 68).

Ornament on the inner whorls consists of prominent bullate to auricular umbilical tubercles, weak prorsiradiate ribs and rounded to clavate ventrolateral tubercles. The latter are situated near the ventral third of the flanks. In the

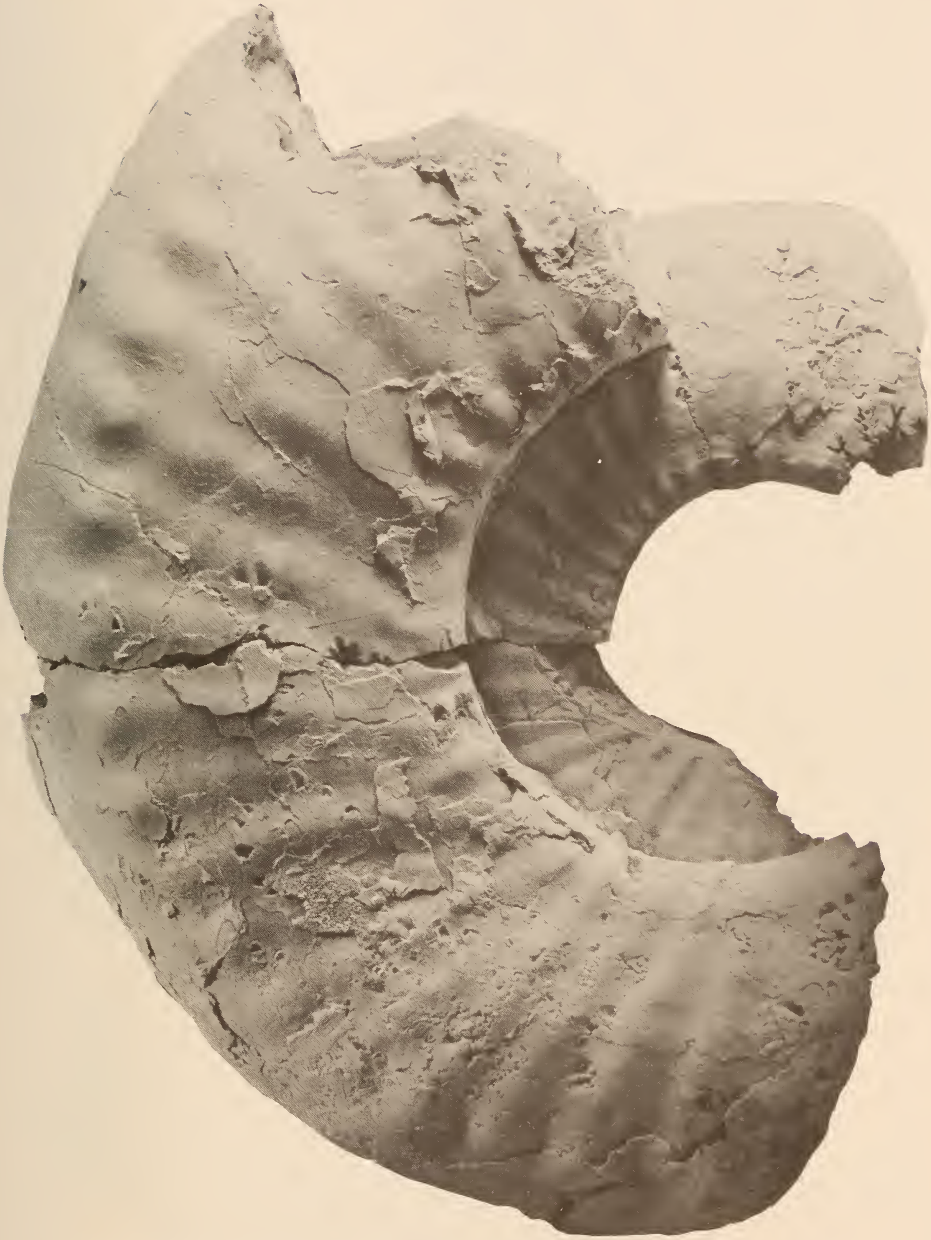

Fig. 70. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z733, the holotype of Van Hoepen's *P. (Zuluites) georgemeintjesi*. × 0,66.

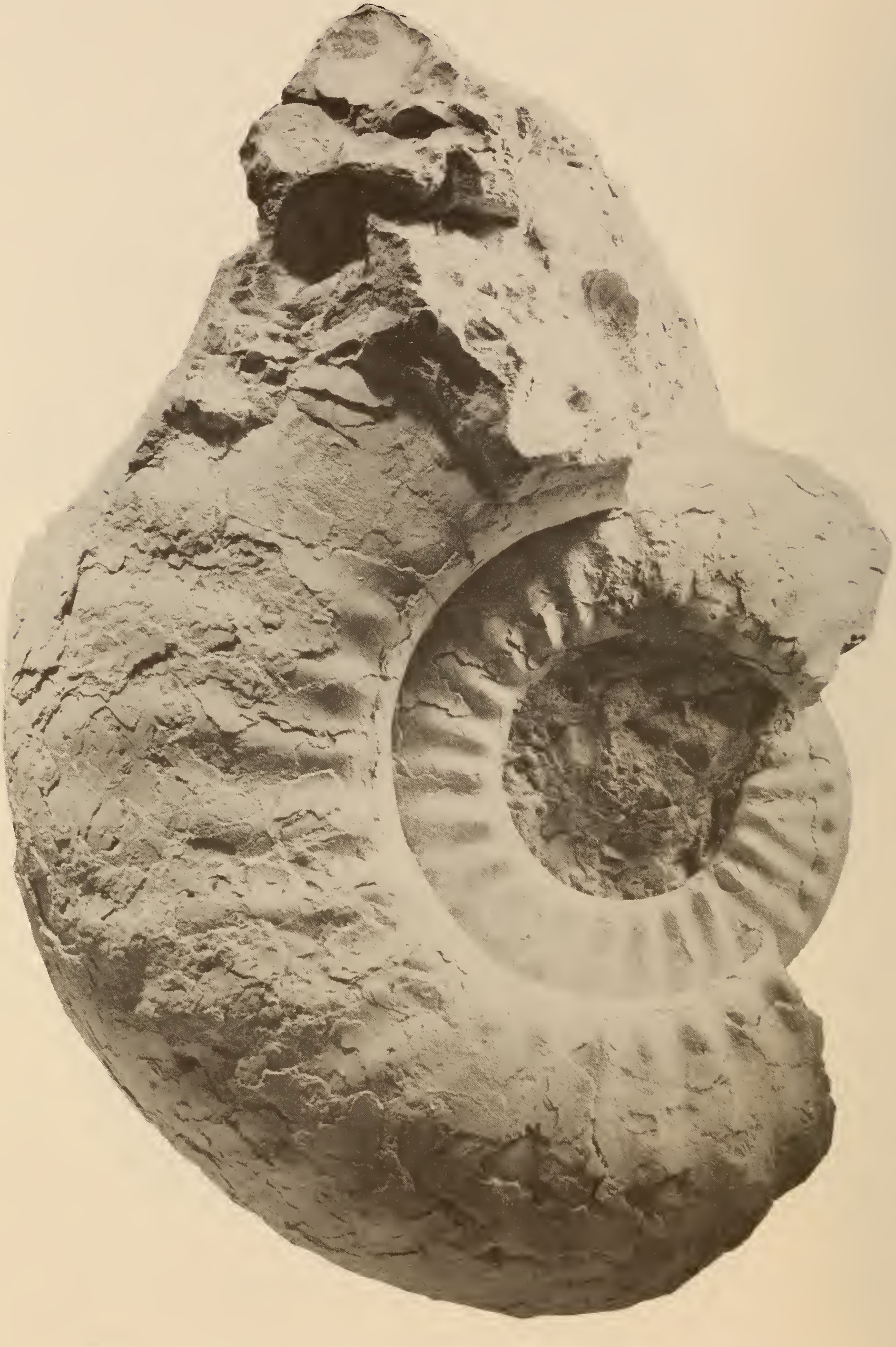

Fig. 71. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z185, the holotype of *P. (Zuluites) lettiae* van Hoepen, 1965. × 1.

fastigiate area between the ventrolateral tubercles and the central keel, numerous spiral striae occur. In some specimens, e.g. SAS Z15 (Fig. 73), these striae also cover the ventrolateral tubercles. The central keel undulates, but the undulations do not coincide with ventrolateral clavi. The central keel is bounded on either side by a shallow depression producing slight spiral ridges, but these can hardly be termed lateral keels.

On the outer whorls of the specimens available (nearly all of them are still septate), all ornament weakens and the whorls become nearly smooth.

Discussion

P. (Zuluiceras) undulatocarinatum continues the trend towards increased involution and compression, forming a link between *P. (Z.) henniei* and *P. (Z.) modestum*. In addition, loss of ornament on the outer whorls is obvious. This is comparable to that found in the transition from *Texanites* to *Submortoniceras* (Klinger & Kennedy 1980: 172).

Differences between *undulatocarinatum, henniei* and *modestum* are gradational in some respects. There is no clear-cut boundary between them in respect of umbilical diameter: *P. (Z.) henniei* has an umbilical width of 40 to 45 per cent, *P. (Z.) undulatocarinatum* between 35 and 40 per cent, whereas *P. (Z.) modestum* has an umbilical width below 30 per cent. These reductions in umbilical width are, however, accompanied by changes in whorl section and loss of ornament.

P. (Zuluiceras) undulatocarinatum, as here interpreted, includes *P. (Zuluites) georgemeintjesi* van Hoepen and *P. (Z.) lettiae* van Hoepen. Differences between these latter 'species' and *P. (Zuluiceras) undulatocarinatum* are minor and restricted to details of the inner whorls.

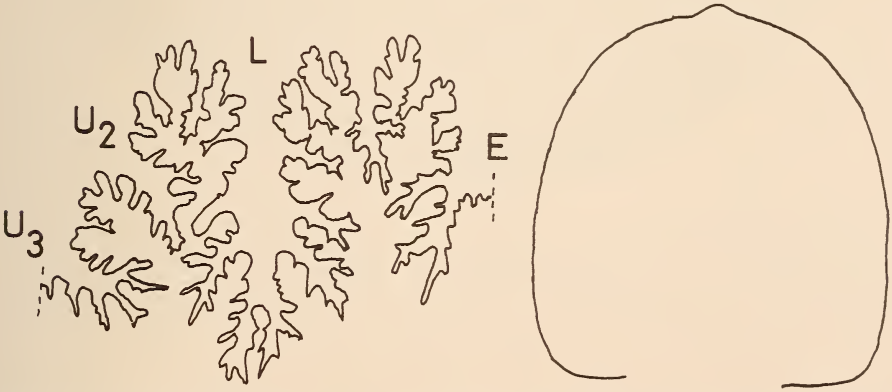

Fig. 72. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. Suture-line and whorl section of SAS Z185, the holotype of *P. (Zuluites) lettiae* van Hoepen, 1965. × 1. (After Van Hoepen 1965, figs 7d, a.)

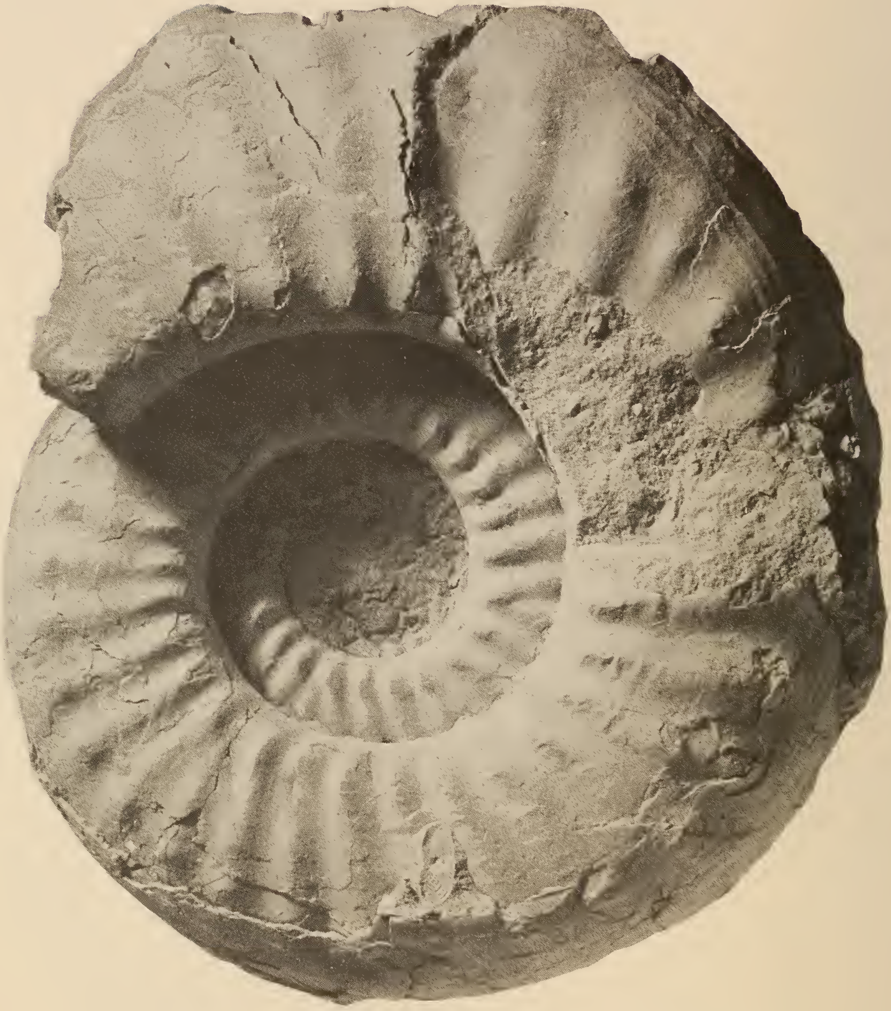

Fig. 73. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z15, the holotype. × 0,72.

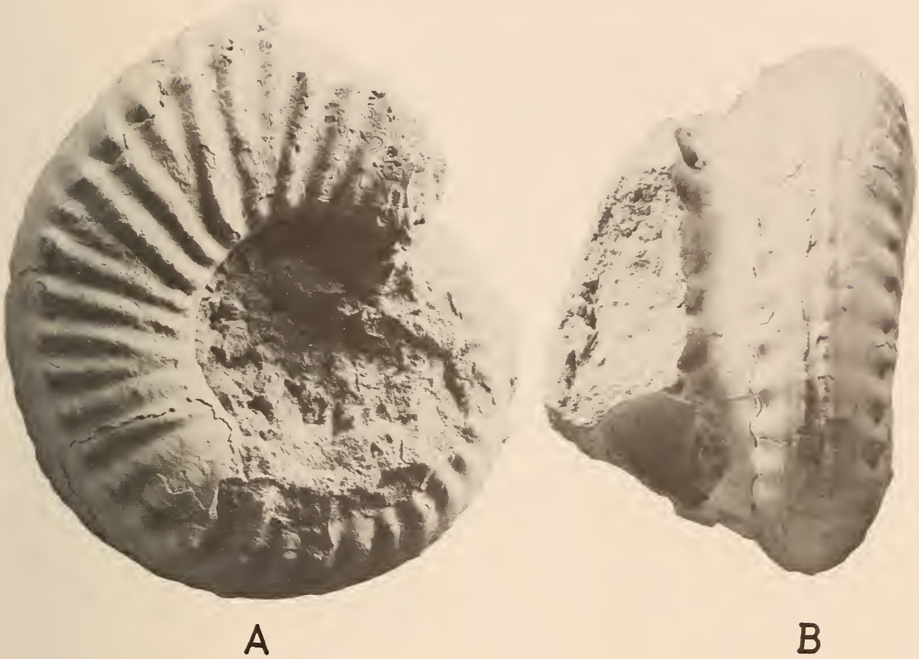

Fig. 74. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z733, the inner whorls of *P. (Zuluites) georgemeintjesi* van Hoepen, 1965. × 1.

P. (Zuluites) dubium (Fig. 75) is more compressed than the holotype of *P. (Zuluiceras) undulatocarinatum* and has finer ornament. It bears great similarity to the inner whorls of the holotype of *P. (Zuluites) georgemeintjesi* (Fig. 74), The outer whorls of the latter are, however, virtually identical with those of *P. (Zuluiceras) undulatocarinatum*. The holotype of *P. (Zuluites) lettiae* (Figs 71–72) has stouter, more quadrate inner whorls than the holotype of *P. (Zuluiceras) undulatocarinatum* and is in these respects transitional to *P. (Z.) henniei* and *P. (Z.) zulu*.

In summary, inner whorls are rather variable as far as dimensions and ornament are concerned; this is analogous to the situation in the similarly compressed *Submortoniceras condamyi* Collignon, 1948, and *S. woodsi* (Spath, 1921), from Zululand and Pondoland (Klinger & Kennedy 1980).

Occurrence

The type locality is strewn with rubble from divisions Coniacian IV and V, the species probably coming from the former level.

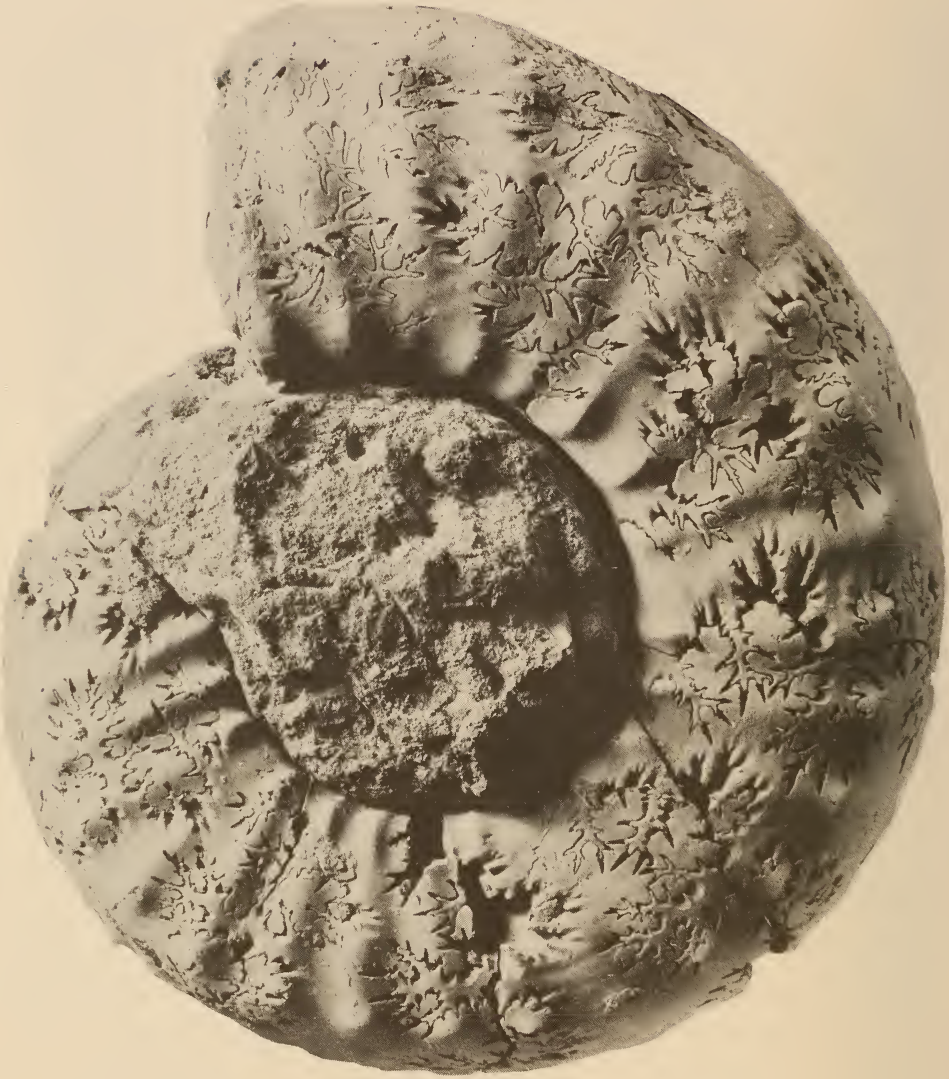

Fig. 75. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1955. SAS Z750, the holotype of *P. (Zuluites) dubium* van Hoepen, 1965. × 1.

Peroniceras (Zuluiceras) modestum van Hoepen, 1965

Figs 76–85

Peroniceras (Zuluites) modestum van Hoepen, 1965: 24, pl. 19, text-fig. 6a–b.

Type specimen

The holotype, by original designation, is SAS Z739 (Fig. 76, 77A) from locality 91, degraded river cliffs and artificial cut west of the boundary of St. Lucia Game Reserve and Lot H103, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, probably Coniacian IV.

Material

SAS Z21, Z104, Z379, Z631, and Z868 from the same locality and inferred horizon as the holotype, SAS 106 from locality 89, St. Lucia Formation, Coniacian IV. BMNH C83863 and C83864 from the same horizon at locality 82.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z868	145,0	49,0(33,8)	59,9(40,7)	0,83	49,0(33,8)	28:35
SAS106	152,0	51,0(33,6)	67,0(44,1)	0,76	42,0(27,6)	—
Z739	160,0	57,0(35,6)	72,0(45,0)	0,79	46,0(28,7)	—
Z379	165,0	56,0(33,9)	74,0(44,8)	0,76	50,0(30,3)	—
SAS104	229,0	64,0(27,9)	102,0(44,5)	0,63	59,0(25,8)	—

Description

Coiling is very involute, the umbilical diameter varying between 25 and 33 per cent, and up to 50 per cent of the previous whorl being covered.

The whorl section is compressed ovoid throughout ontogeny, with a vertical to distinctly overhanging umbilical wall, slightly inflated flanks converging to a broadly rounded venter, with no distinct demarcation between the latter and the flanks. The venter bears one narrow, serrated keel. Slight depressions occur on either side of the keel, especially on the inner whorls, but distinct lateral keels are not developed. On the outer whorls of the phragmocone these depressions virtually disappear and the venter is unicarinate without sulci.

Ornament on the inner whorls is as in *P. (Z.) undulatocarinatum*, but rapidly disappears on the outer whorls, leaving the shell completely smooth but for slight undulations representing the umbilical tubercles. Spiral striae occur on the ventral regions where the shell is well preserved.

All the specimens are still septate, indicating that the species grew to a very large size. The suture is of the *P. (P.) dravidicum* type.

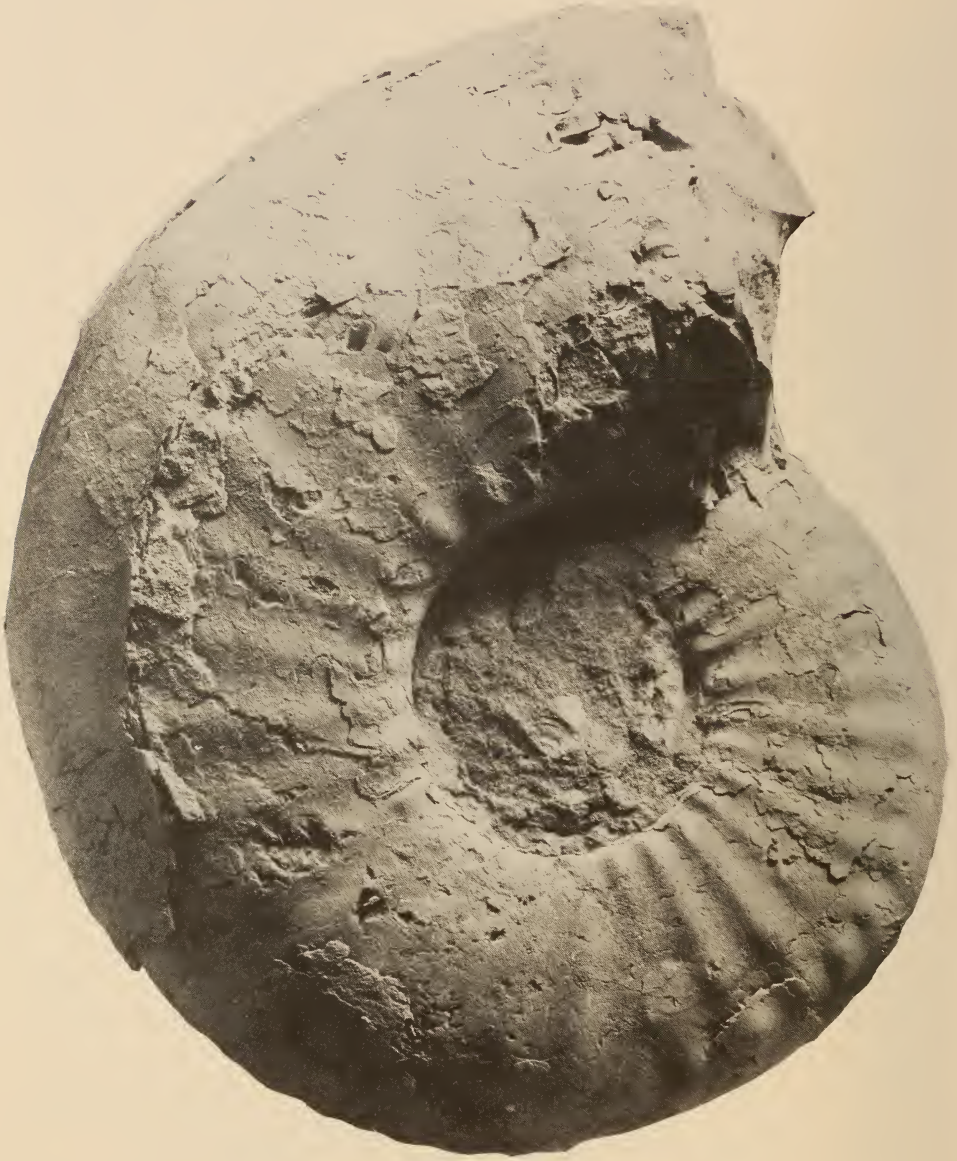

Fig. 76. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z739, the holotype. × 1.

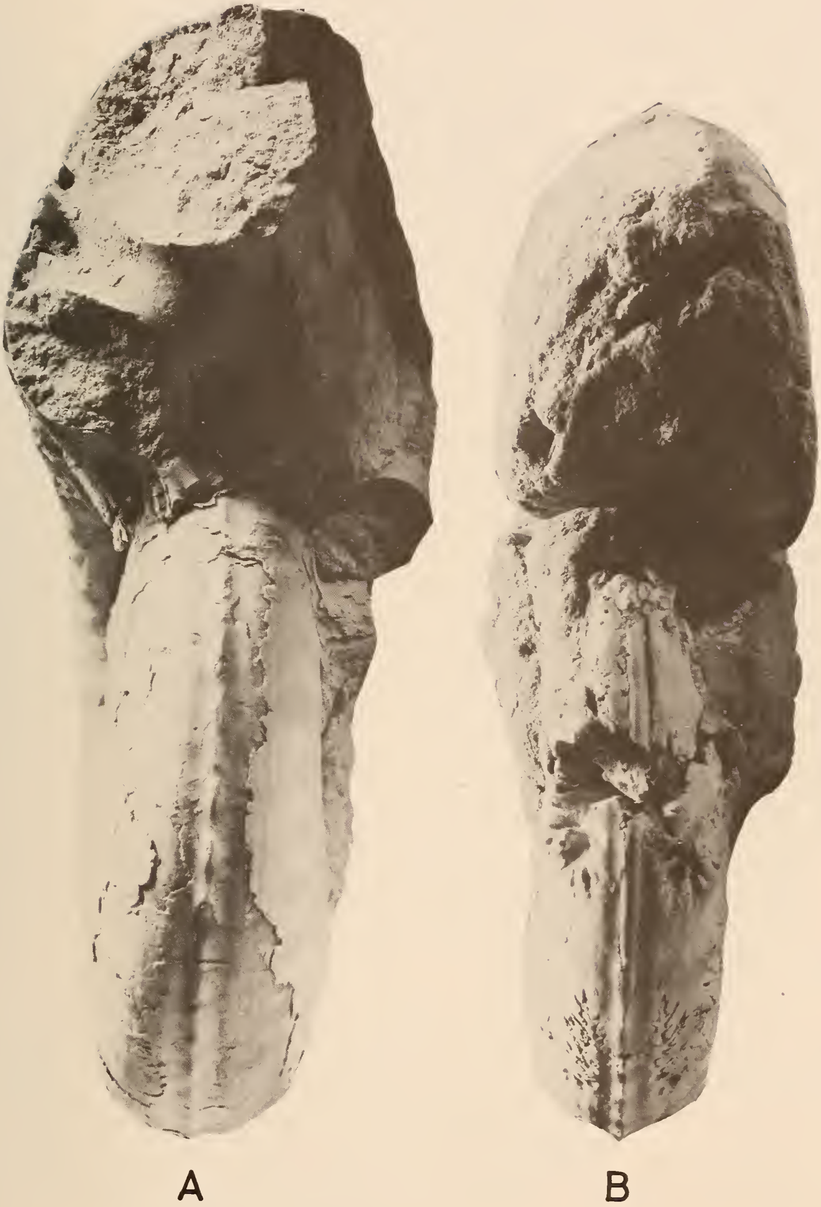

Fig. 77. A. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z739. B. *Peroniceras (Zuluiceras) undulatocarinatum* van Hoepen, 1965. SAS Z750, the holotype of *P. (Zuluites) dubium* van Hoepen, 1965. Both × 0,92.

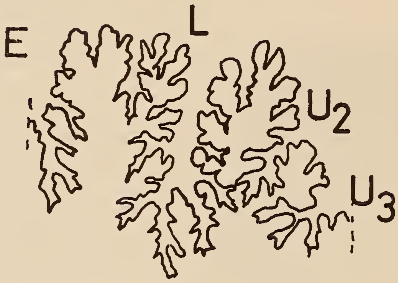

Fig. 78. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965.
Suture-line of the holotype. × 1.
(After Van Hoepen 1965, fig. 6a.)

Discussion

This species is easily distinguished from the preceding *Peroniceras (Zuluiceras)* species by the high degree of involution and virtual lack of ornament on the later whorls of the phragmocone.

This appears to be the last species of the *P. (P.) dravidicum* stock, a line that evolved rapidly through the Middle and lower Upper Coniacian in Zululand, becoming progressively larger and showing increasing involution and whorl compression, losing lateral ornament and the pair of lateral keels. Although the end member is very different from the ancestral *P. (P.) dravidicum*, the suture-line remained remarkably similar throughout, especially the U_2/U_3 lateral saddle, which remained attached obliquely by a thin stem to the root of the lateral L/U_2 saddle.

Occurrence

Coniacian IV of Zululand.

Peroniceras (Zuluiceras) matsumotoi sp. nov.

Figs 86–88

Type specimen

The holotype is NMB D1140 from locality 73, degraded river cliffs on the north bank of the Mzinene River downstream of the junction with the Munywana River, Zululand, St. Lucia Formation, probably Coniacian IV.

Etymology

The species is named for Emeritus Professor Tatsuro Matsumoto of Kyushu University.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
D1140	168,0	40,0(23,8)	52,0(30,9)	0,77	76,0(45,2)	—

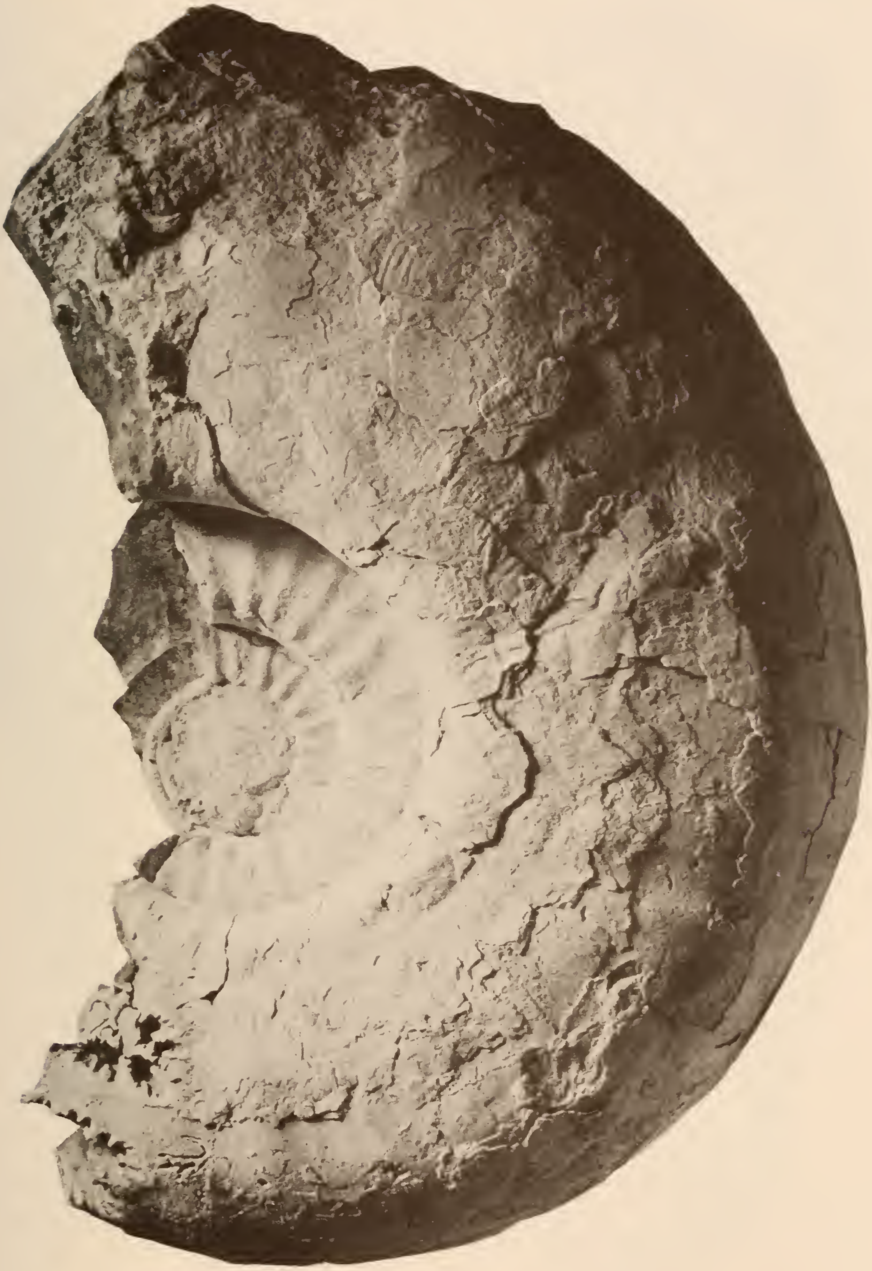

Fig. 79. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z743. Note the similarity to *P. (Z.) matsumotoi* sp. nov. (Figs 86–88) apart from the more inflated whorl section and narrower umbilical width. × 0,68.

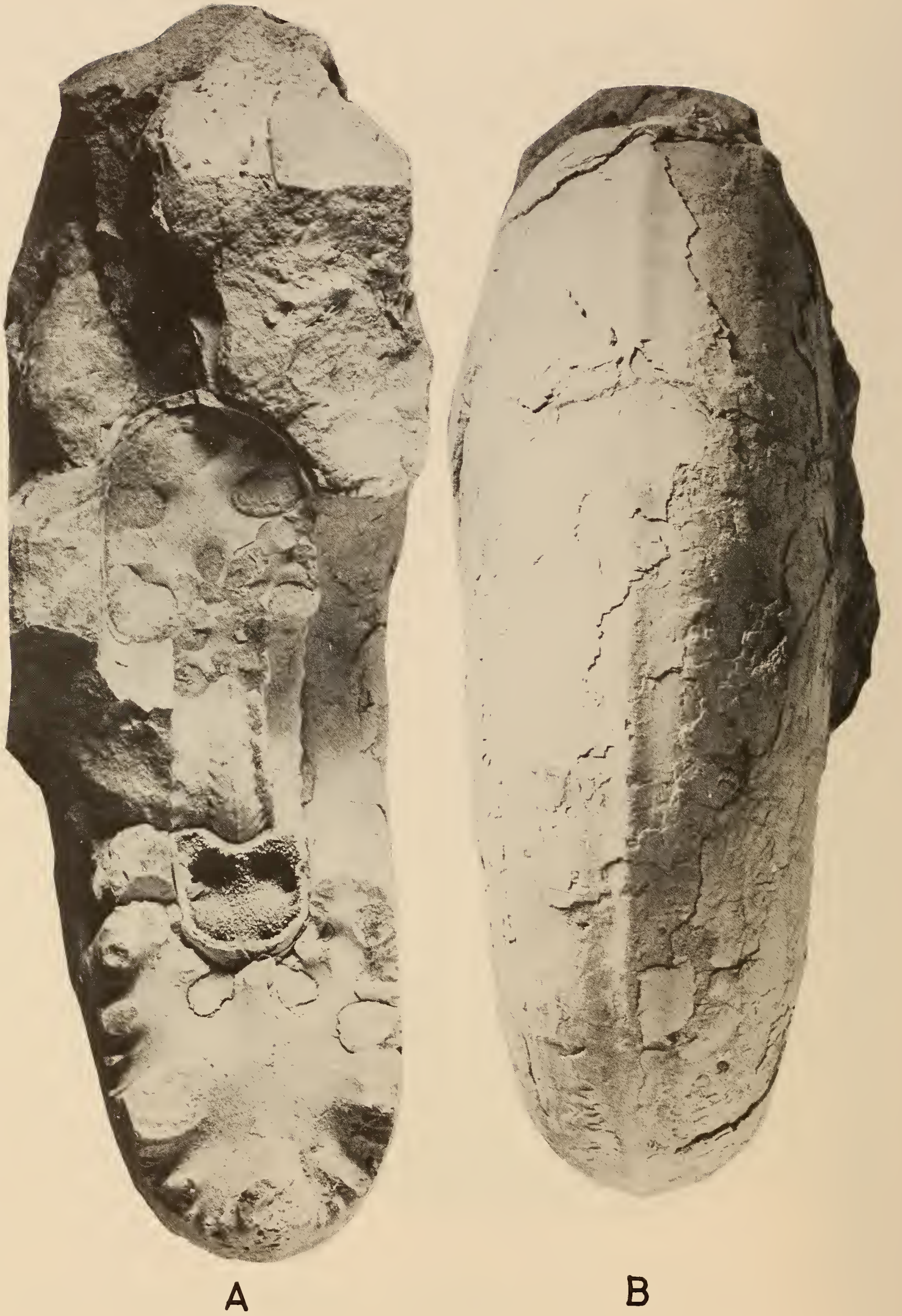

Fig. 80. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z743. Note the serrated, unicarinate venter already present on the inner whorls. × 0,71.

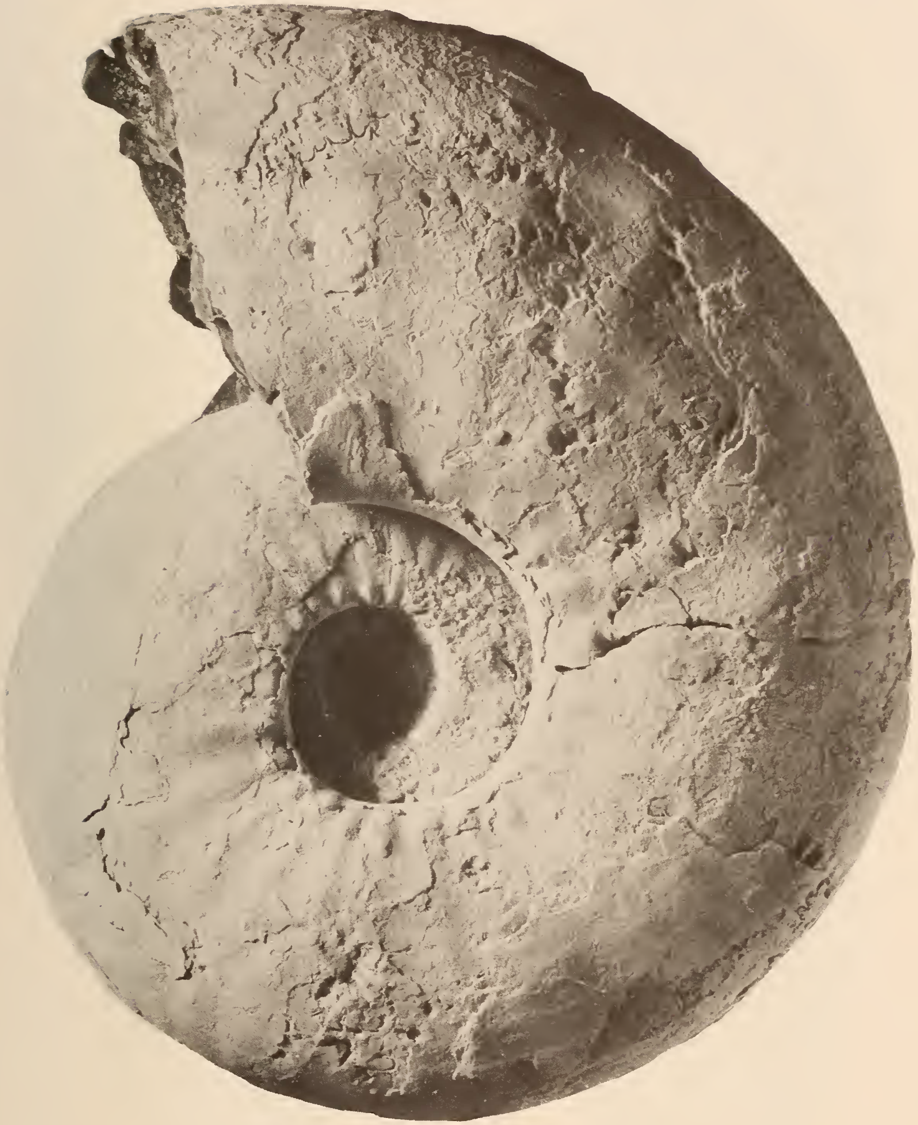

Fig. 81. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 104. × 0,67.

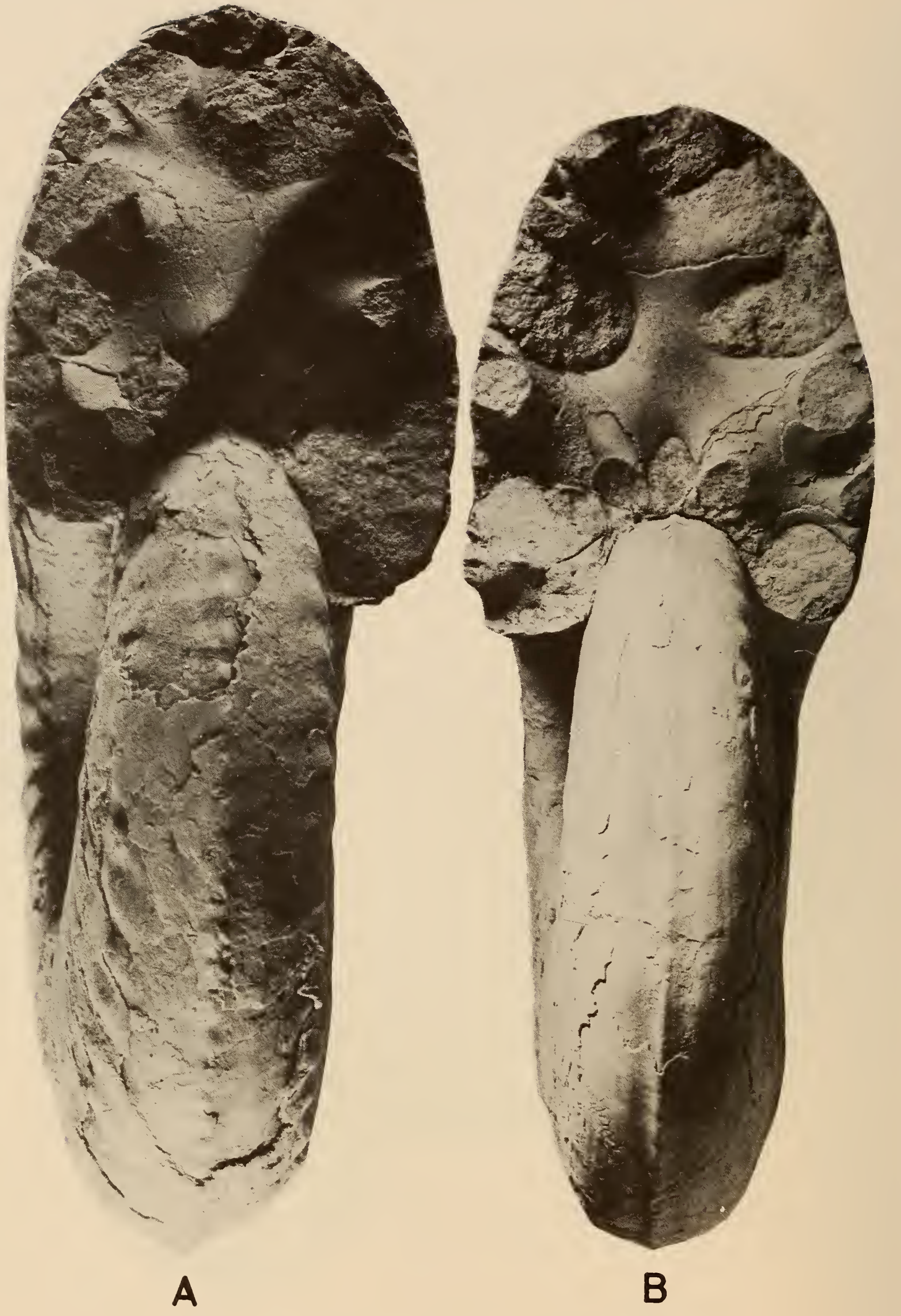

Fig. 82. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965.
A. SAS Z868. × 1 B. SAS 104. × 0,69.

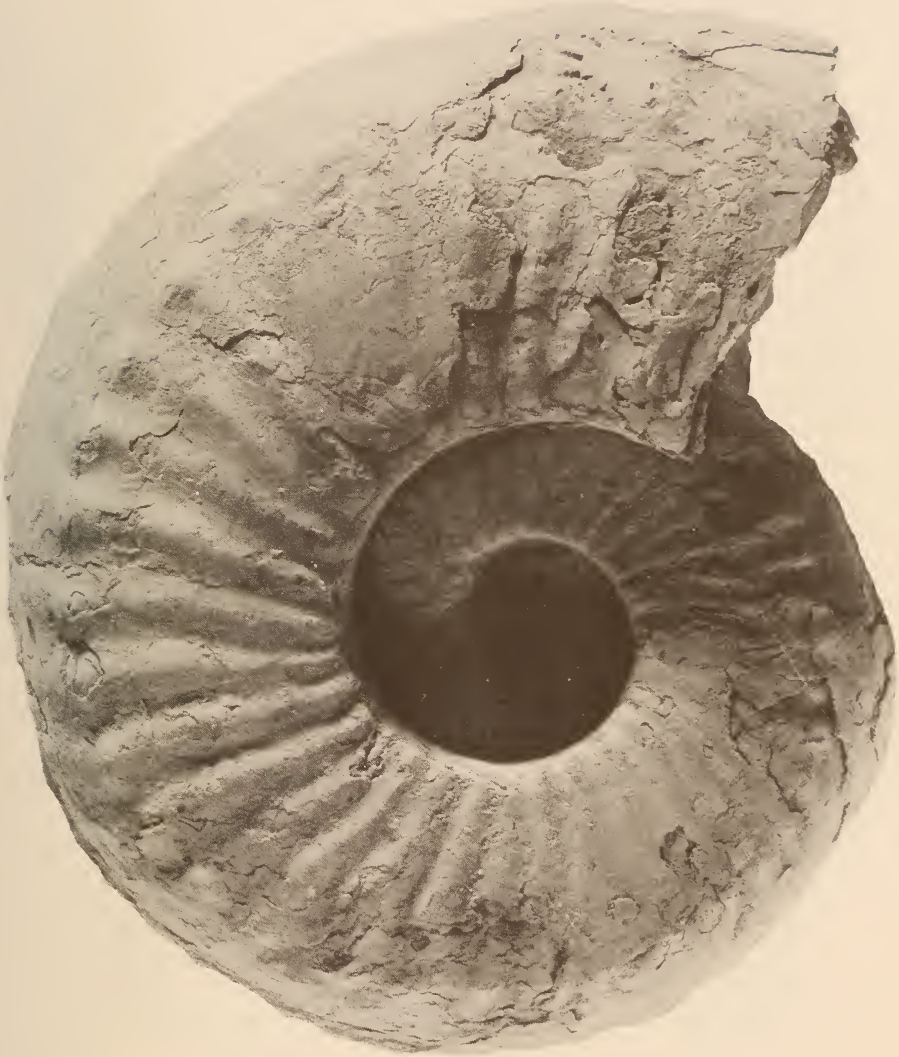

Fig. 83. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS Z868. × 1.

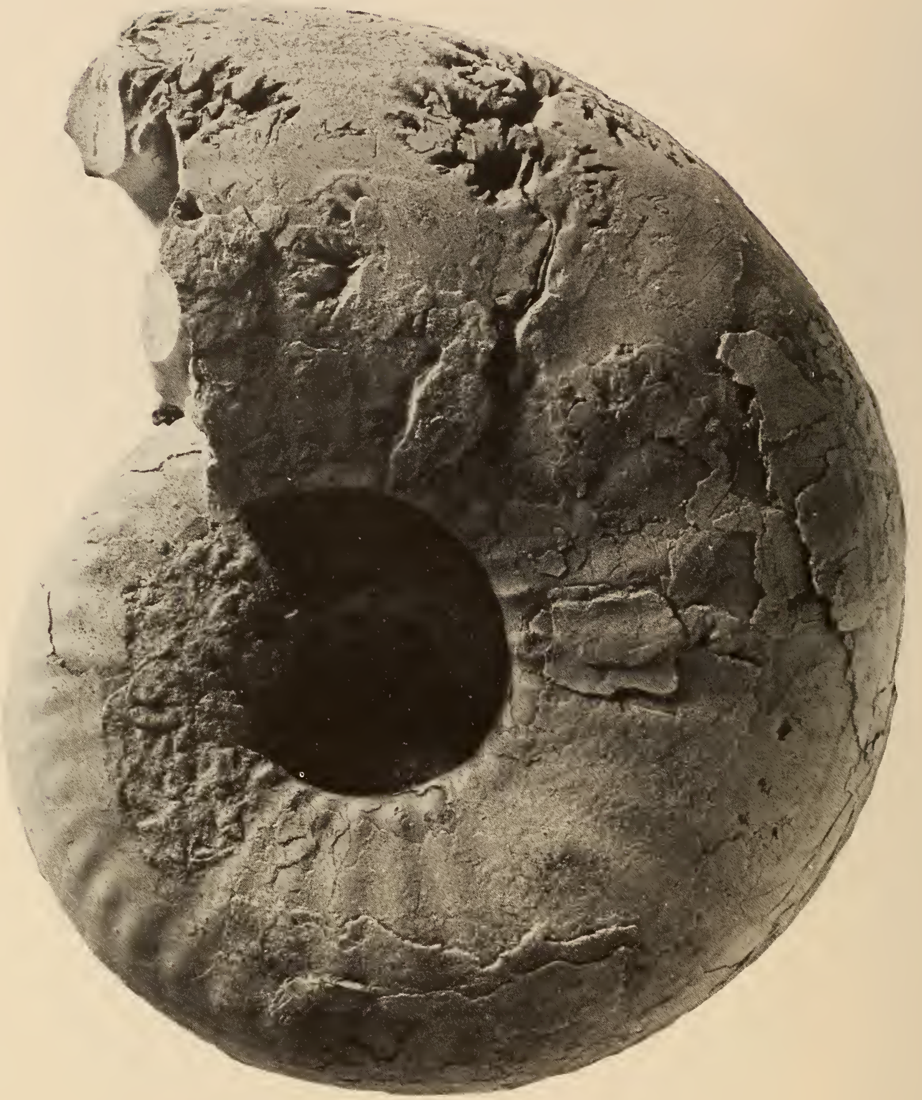

Fig. 84. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 106. × 1.

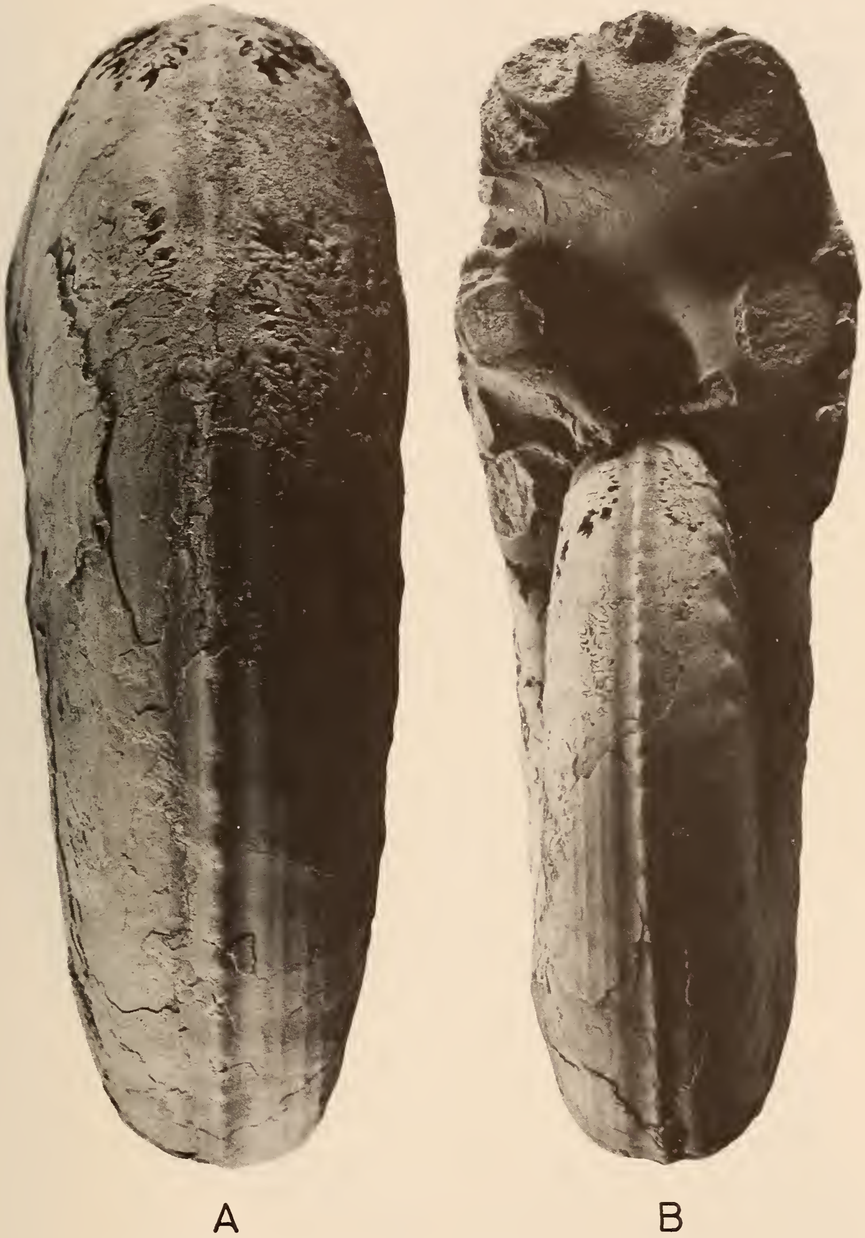

Fig. 85. *Peroniceras (Zuluiceras) modestum* van Hoepen, 1965. SAS 106. × 1.

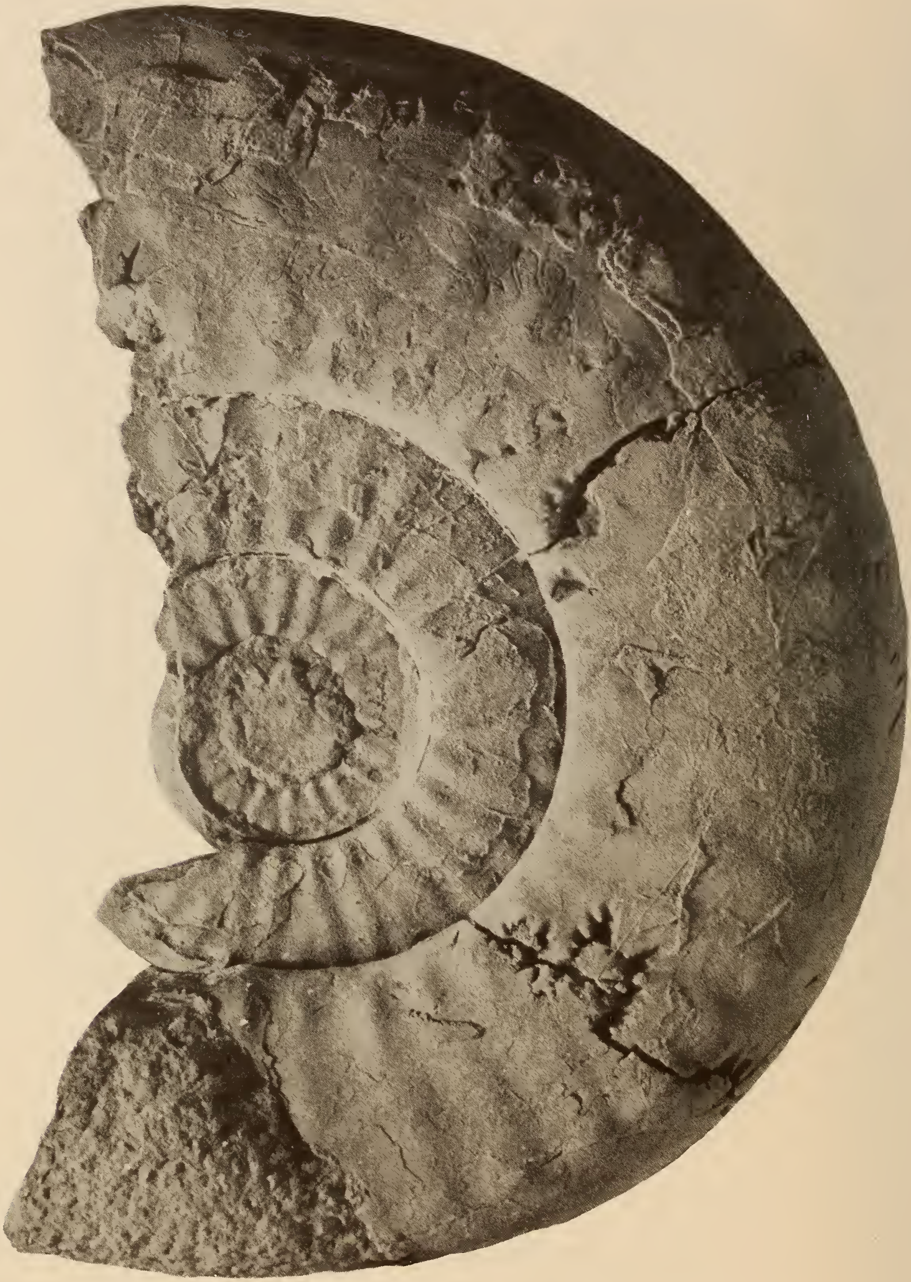

Fig. 86. *Peroniceras (Zuluiceras) matsumotoi* sp. nov. Holotype NMB D1140. × 1.

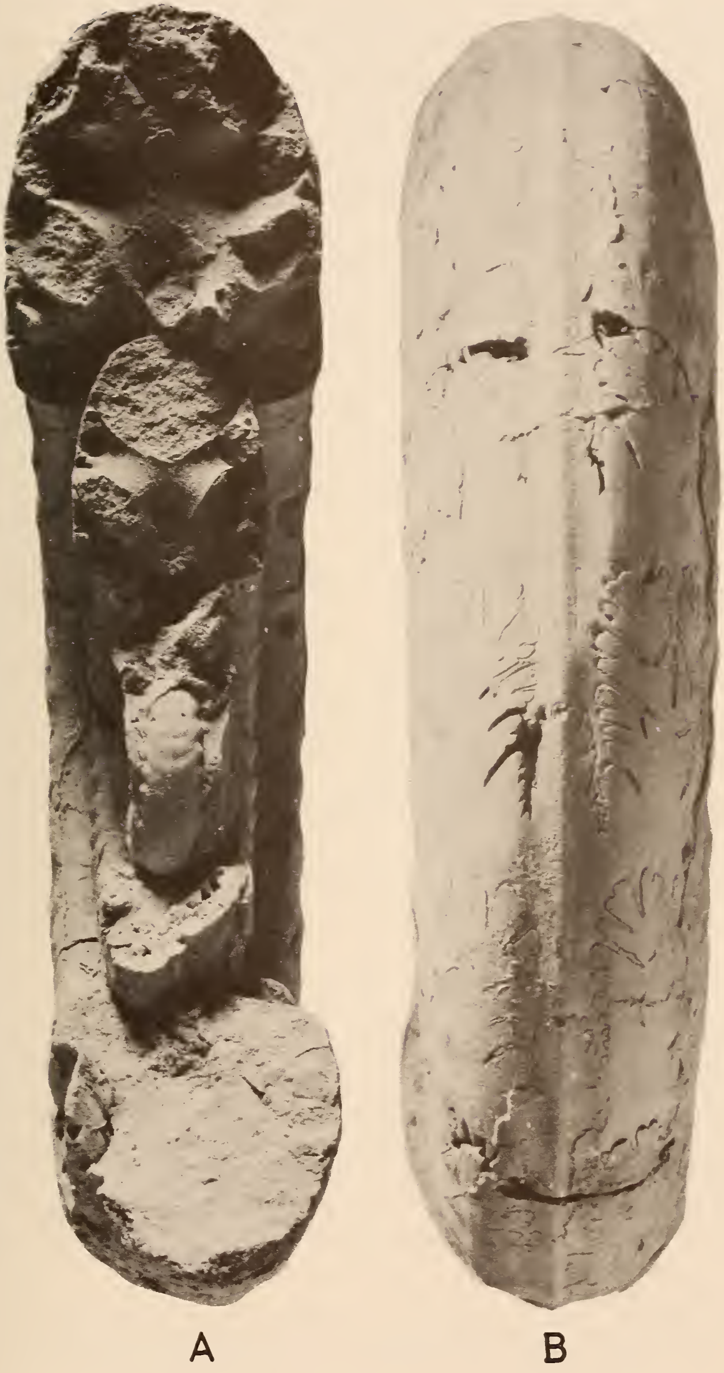

Fig. 87. *Peroniceras (Zuluiceras) matsumotoi* sp. nov.
Holotype NMB D1140. × 1.

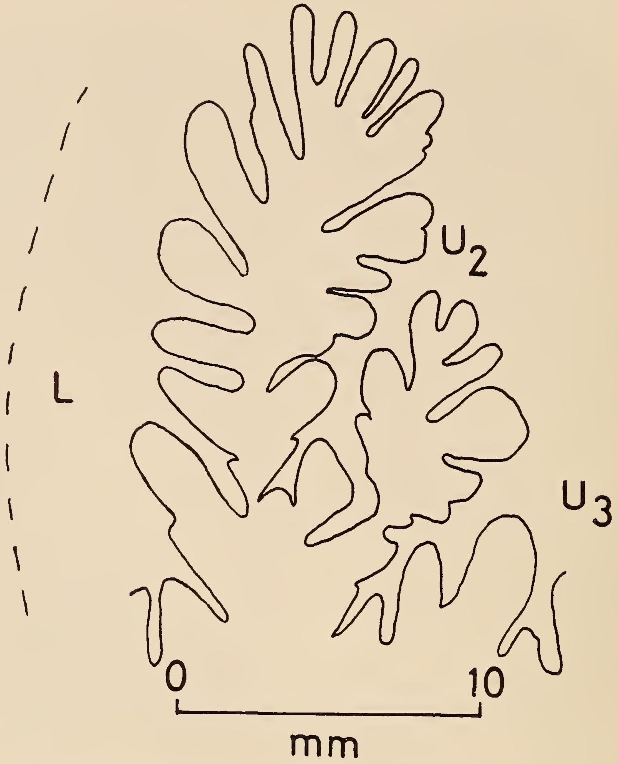

Fig. 88. *Peroniceras (Zuluiceras) matsumotoi* sp. nov. Suture-line of holotype NMB D1140.

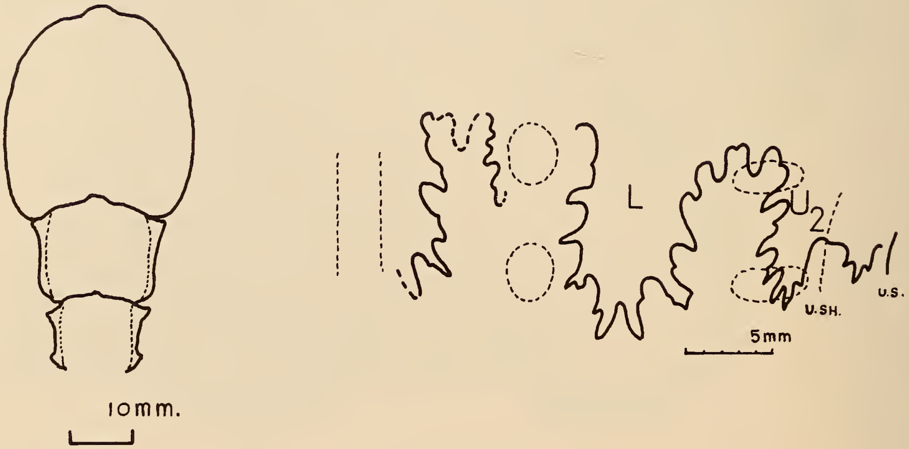

Fig. 89. *Ishikariceras binodosum* Matsumoto, 1965. Whorl section and partical suture. × 1. (After Matsumoto 1965, text-figs 17–18.)

Description

Coiling is very evolute, with only 25 to 33 per cent of the preceding whorl covered, the degree of overlap increasing through development. The umbilical diameter is 45 per cent of the total diameter.

The whorl section is compressed throughout, with subparallel, slightly inflated flanks and a broadly rounded unicarinate venter. The venter is unicarinate at the smallest diameter observed but in later growth it is bound by shallow depressions, although no distinct lateral keels develop. The keel is serrated on the inner whorls but entire on the internal mould of the outer whorls.

The ornament of inner whorls consists of umbilical bullae and rounded ventrolateral tubercles. These are linked by radial ribs, most of which are single, with only occasional bifurcations at or near the umbilical tubercle. Ornament weakens progressively in later growth and, at the greatest diameter preserved, the flanks bear only feeble undulations. The suture is incompletely exposed (Fig. 88) but is of the *P. (P.) dravidicum* type. The body chamber is unknown.

Discussion

P. (Z.) matsumotoi differs from all the other Zululand species in being both compressed and very evolute.

The precise relationship of this species to other *P. (Zuluiceras)* species is not clear, as transitional or superficially similar forms do not occur.

The most similar form occurs in Madagascar: '*Schloenbachia*' *schneeblii* Boule, Lemoine & Thévenin (1907: 36, pl. 5 (figs 2–2a), text-fig. 20). It resembles *P. (Z.) matsumotoi* in having coarse ornament on the inner whorls but virtually smooth, unicarinate outer phragmocone whorls. At comparable diameters, however, the suture-lines are totally different. That of '*Schloenbachia*' *schneeblii* is very simple, with broad parallel saddles and lobes, markedly different from the highly incised, narrow saddles and lobes of *P. (Z.) matsumotoi*. Moreover, the siphonal keel of '*Schloenbachia*' *schneeblii* is both broader and more prominent than that of *P. (Z.) matsumotoi*.

Another comparable form is *Ishikariceras binodosum* Matsumoto (1965: 236, pl. 43 (fig. 1), text-figs 17–18) from the Coniacian of Hokkaido, Japan. The inner whorls have a more quadrate section but the Japanese species show the same loss of ornament on the outer whorls. The suture of the Japanese species is strikingly different from that of *P. (Z.) matsumotoi* and is simple, with little-incised, broad elements (Fig. 89). This is a situation comparable to that between the extremes of *Peroniceras* s.s. Here, however, no intermediate forms linking *Ishikariceras* to *Peroniceras* are known. Although it seems probable that such forms will turn up, retention of *Ishikariceras* as a separate genus seems wise at present.

Other comparable forms are two specimens described by Matsumoto (1965: 233) as *Sornayceras* sp. cf. *propoetidum* from the 'Upper' Coniacian of Hokkaido, Japan. These specimens have suture-lines and whorl sections like those of the present species, but are more narrowly umbilicate (U = only 30 per cent of the total diameter as against 45 per cent in *P. (Z.) matsumotoi*)

Occurrence

Coniacian IV of Zululand only.

Peroniceras (Zuluiceras) cf. *aberlei* (Redtenbacher, 1873)

Figs 90–91, 92A

Compare

Ammonites aberlei Redtenbacher, 1873: 111, pl. 25 (fig. 4a–e).
De Grossouvre, 1894: 89.

Type specimen

Redtenbacher failed to designate a holotype for this species. A lectotype designation will be undertaken in a pending version of some of the Gosau faunas (Kennedy & Summesberger in preparation).

Material

NMB D1147 from locality 72, degraded river cliff and stream sections on the north side of the Mzinene River downstream of the junction of the Munywana River, Zululand, St. Lucia Formation, Coniacian II or III.

Description

A single specimen consisting of parts of two successive septate whorls is referred to Redtenbacher's species. The section of both whorls is distinctly compressed, with a fastigiate venter bearing a single keel. The keel appears entire and is bounded on either side by distinct grooves, creating the appearance of weak lateral keels. Ornament on the inner whorls consists of fine, frequently bi-

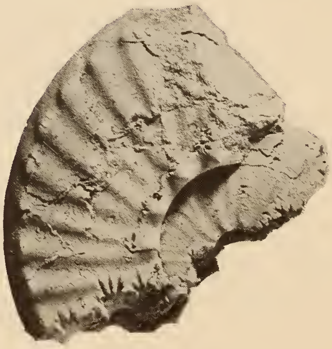

Fig. 90. *Peroniceras (Zuluiceras) cf. aberlei* (Redtenbacher, 1873). NMB D1147. × 1.

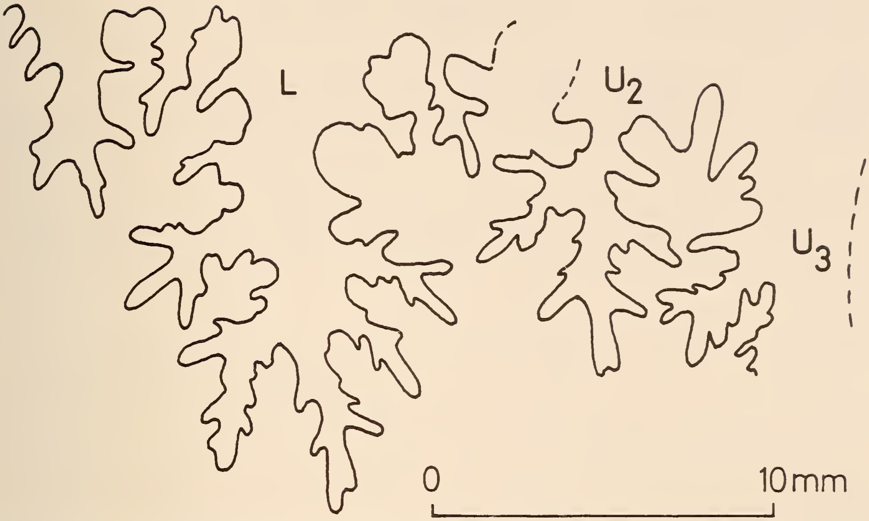

Fig. 91. *Peroniceras (Zuluiceras) cf. aberlei* (Redtenbacher, 1873). Suture-line of NMB D1147.

furcating, prorsiradiate ribs. On the outer whorl, ornament is coarser and the umbilical tubercles are very prominently rounded to slightly auricular.

The suture is highly incised and of the *P. (P.) dravidicum* type (Fig. 91).

Discussion

Redtenbacher based this species on a series of specimens; a cast of one of these is here illustrated as Figure 92A. A full discussion of the species is to be given in a forthcoming revision of the Gosau Fauna (Kennedy & Summesberger in preparation). *P. (Z.) aberlei* can be distinguished from the similarly compressed *P. (Z.) propoetidum* (Redtenbacher, 1873) and *P. (Z.) bajuvaricum* (Retenbacher, 1873) by virtue of its fewer, coarser ribs and tubercles, more of which arise in pairs from the umbilical bullae. *P. (Z.) proteus* (Matsumoto, 1965) is much more coarsely ornamented than *P. (Z.) aberlei.*

Occurrence

Coniacian of western and southern Europe, and Zululand.

Peroniceras (Zuluiceras) bajuvaricum (Redtenbacher, 1873)

Figs 92B–C, 93

Ammonites bajuvaricus Redtenbacher, 1873: 107, pl. 24 (fig. 2a–c).
Gauthiericeras bajuvaricum (Redtenbacher): de Grossouvre, 1894: 88, pl. 9 (fig. 1), pl. 12 (figs 2a–b, 3a–b), text-fig. 35.
Schloenbachia (Gauthiericeras) bajuvarica (Redtenbacher): Boule, Lemoine & Thévenin, 1907: 22, pl. 12 (fig. 1—1a), text-fig. 22.
Gauthiericeras bajuvaricum (Redtenbacher): Diener, 1925: 152 (with synonomy).

Gauthiericeras bajuvaricum (Redtenbacher) var. *skoenbergensis* Venzo, 1936: 105, pl. 9 (fig. 5), pl. 11 (fig. 7).
Sornayceras bajuvaricum (Redtenbacher): Matsumoto, 1965: 226 et seq.
Sornayceras omorii Matsumoto, 1965: 230, pl. 42 (figs 1–2), text-figs 13–15.
Sornayceras aff. *bajuvaricum* (Redtenbacher): Szász, 1976: 208, pl. 5 (fig. 2).
Sornayceras cf. *bajuvaricum* (Redtenbacher): Atabekjan & Akopjan, 1972: 10, pl. 3 (figs 4–5).

Type specimen

The lectotype is Redtenbacher's (1873 pl. 24 (fig. 2a–c)) original figured specimen from the Gosau Beds of Austria, designated by Reyment (1958: 43).

Material

NMB D1059 and SAS A343 from locality 72, degraded river cliff and northern banks of the Mzinene River downstream of the Munywana River, Zululand, St. Lucia Formation, Coniacian II or III. SAS Z1632a–b from locality 92, bulldozer scrapings and adjacent hillslopes around pumping station on the farm Panplaas, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian II or III.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z1632a	55,0	16,0(29,1)	19,0(34,5)	0,84	22,0(40,0)	11×2:18×2
Z1632b	60,0	17,0(28,3)	21,0(35,0)	0,85	23,0(38,3)	21:31
A343	77,0	19,0(24,7)	26,0(33,8)	0,73	30,0(39,0)	—
D1059	87,0	23,0(26,4)	32,0(36,8)	0,71	35,0(40,2)	—

Description

Coiling is involute with an umbilical diameter of about 38 to 40 per cent of the total diameter, each whorl covering the ventral third of the preceding one. The whorl section is compressed throughout, with flat parallel flanks and a fastigiate venter. The venter bears a strong central keel bounded on either side by a slight depression. There are weak lateral ridges that cannot be termed true lateral keels. The umbilical wall is vertical to overhanging.

Ornament consists of weak umbilical bullae connected to clavate to rounded ventrolateral tubercles by numerous single and bifurcating ribs.

The suture-line is complex with narrow-stemmed saddles of the *P. (P.) dravidicum* type (Fig. 93).

Discussion

In Zululand the species is easily identified by the narrow umbilicus, high, compressed whorl section, unicarinate, fastigiate venter, and ornament consisting of single and bifurcating ribs.

Venzo (1936: 105–106) commented on the simplicity of the suture-line, but sutures that he described appear to be those of juveniles. Suture-lines of specimens of *P. (P.) dravidicum* taken at similar diameters (Fig. 35) appear identical and there can be no doubt that this is, indeed, a representative of *P. (Zuluiceras)*.

Pending the revision of the Gosau material, a discussion of the affinities of the species is omitted, except that the possibility exists that a number of superficially similar, compressed species such as *P. (Z.) omorii* (Matsumoto) (1965: 230, pl. 42 (figs 1a–b, 2a–b)) and *P. (Z.) isamberti* (Fallot) (1885: 232, pl. 2 (fig. 1)) may be mere variants of the species or subspecies only. *P. (Z.) aberlei* is more sparsely ribbed on the outer whorls, as is *P. (Z.) propoetidum* (Redtenbacher, 1873).

Occurrence

Middle Coniacian of western and southern Europe, Armenia and possibly Japan; Coniacian II of Zululand.

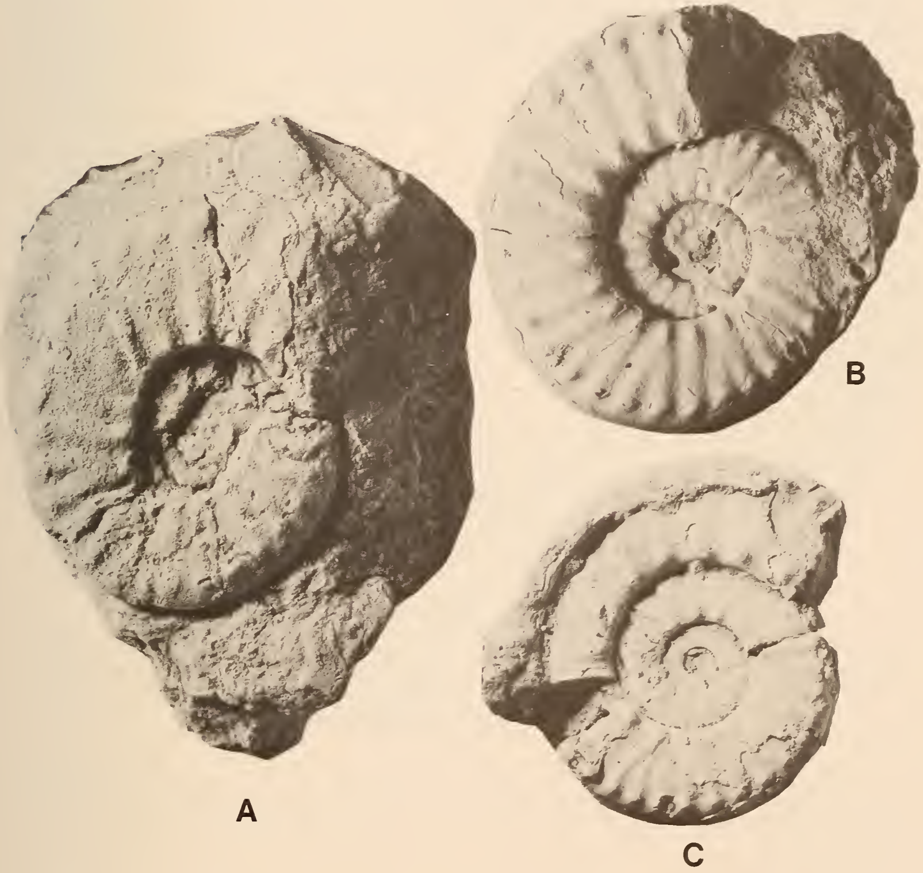

Fig. 92. A. *Peroniceras (Zuluiceras) aberlei* (Redtenbacher, 1873). Cast of one of Redtenbacher's original specimens from the Oberösterreichisches Landesmuseum, Linz. B–C. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). B. SAS Z1632a C. SAS A343. All × 1.

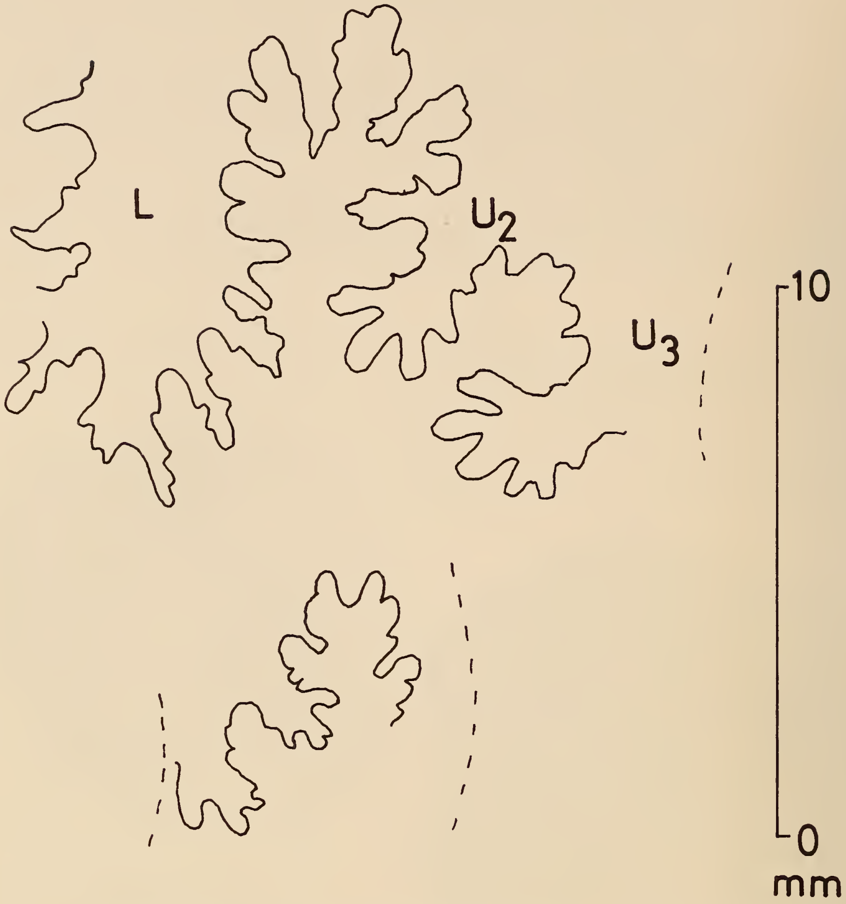

Fig. 93. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). Suture-lines of SAS Z1632a.

Genus *Gauthiericeras* de Grossouvre, 1894

(= *Ciryella* Wiedmann, 1960: 763; *Andersonites* van Hoepen, 1965: 29; *Fluminites* van Hoepen, 1965: 31; *Hluhluweoceras* van Hoepen, 1965: 33; *Falsebayites* van Hoepen, 1965: 34)

Type species

Ammonites margae Schlüter, 1867: 29, pl. 5 (fig. 2) by original designation of de Grossouvre, 1894: 87.

Diagnosis

Medium sized to large, moderately evolute to involute, whorl section depressed to compressed, trapezoidal to quadrate with strong, entire, undulating or serrated siphonal keel flanked by a groove on either side, the outer edge of

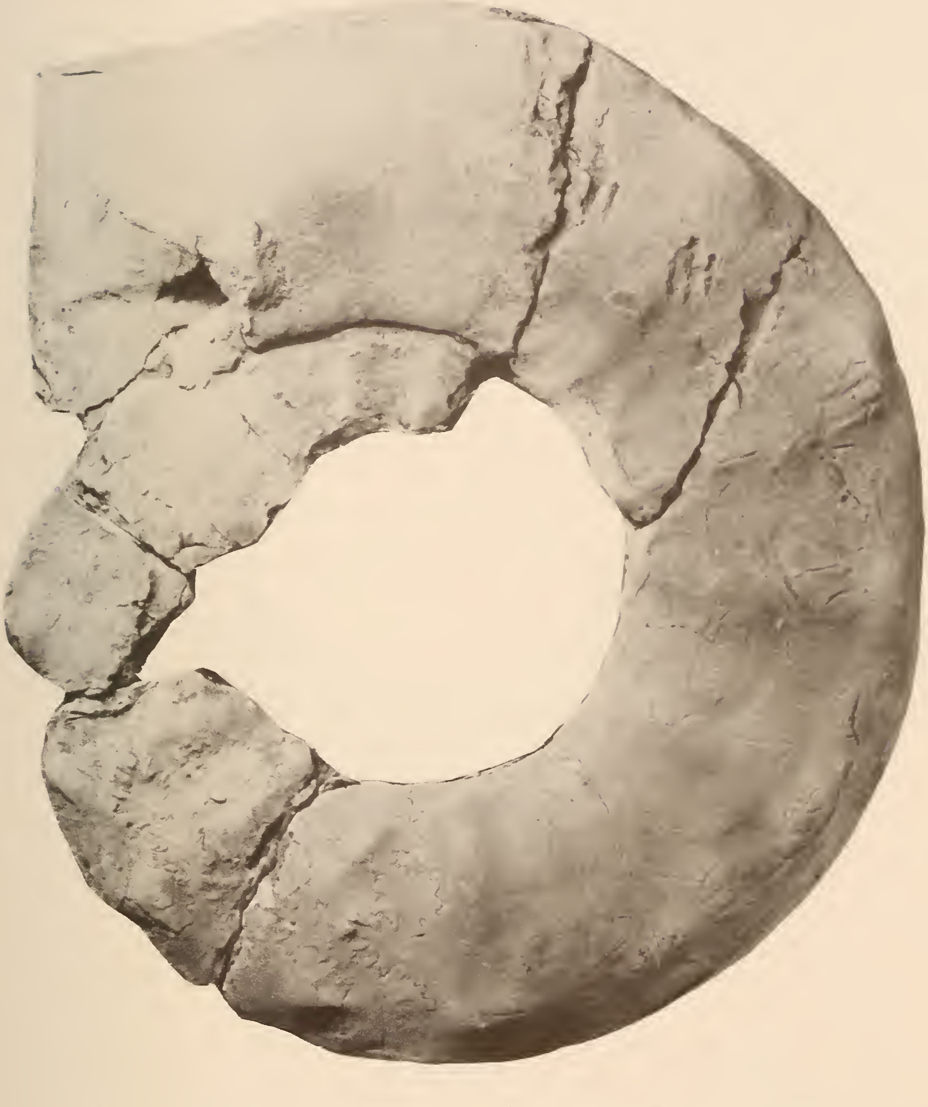

Fig. 94. *Gauthiericeras margae* (Schlüter, 1867). Holotype, the specimen figured by Schlüter (1867, pl. 5 (fig. 2)). × 0,6. (See also fig. 19c.)

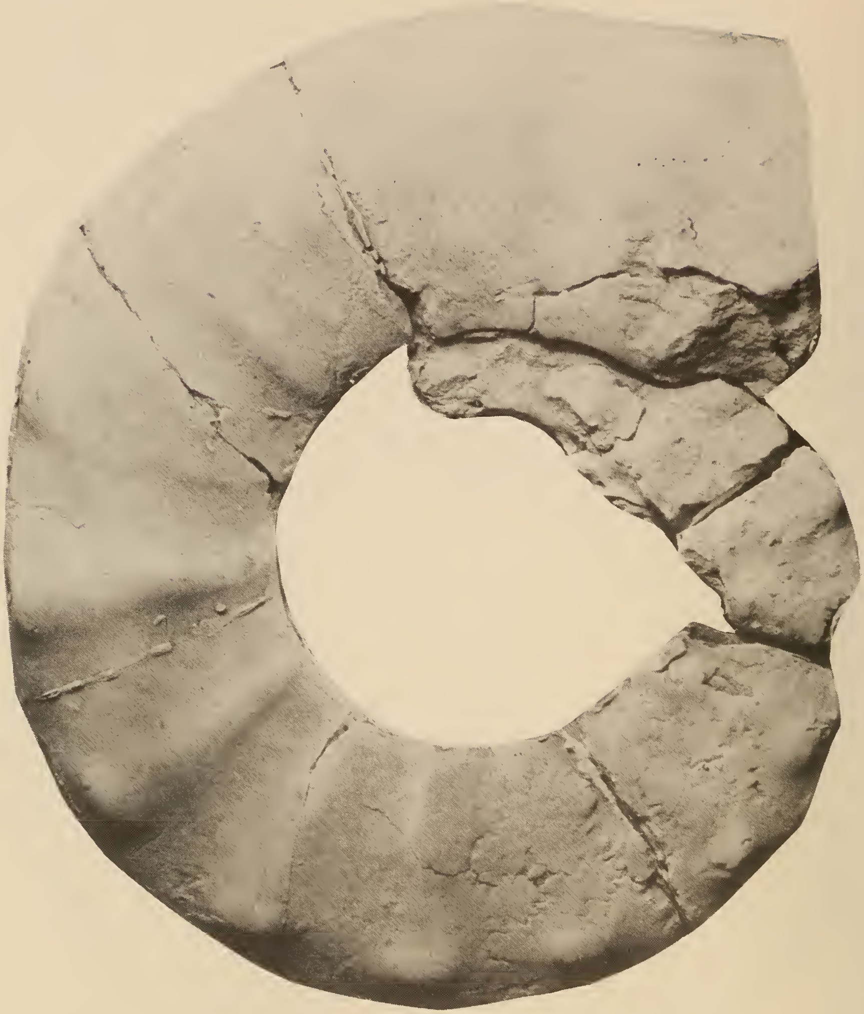

Fig. 95. *Gauthiericeras margae* (Schlüter, 1867). Holotype, the specimen figured by Schlüter (1867, pl. 5 (fig.2)). × 0,6.

which may be strengthened into a low ridge, but not a lateral keel. Strong ribs arise from umbilical bullae in pairs or singly and may branch again from inner to mid-lateral bullae, if present. Shorter intercalated ribs sometimes present. All ribs terminate in strong ventrolateral clavi.

Suture rather simple, with little-incised elements; saddles square.

Discussion

Gauthiericeras is easily distinguished from other peroniceratids by its strong siphonal keel, lack of true lateral keels, strong ribs and the presence, in the type species and some others, of a lateral tubercle. Persistent ornament and paired or branching ribs distinguished it from *Ishikariceras*.

Wiedmann (1960: 763, pl. 8 (figs 1–4), text-fig. 16) introduced the subgenus *Gauthiericeras (Ciryella)*, type species *G. (C.) vascogoticum*. The original diagnosis is as follows: 'Coquille à enroulement extrêmement évolute qui laisse voir les tubercles marginaux. Section de tours rectangulaire. Les côtes restent simples et serrées chez l'adulte et sont munies d'un tubercle ombilical allongé dans le sens de la côte et d'un tubercle marginal en massue. Au stade jeune, les cotes qui couvrent seulement les flancs sont bifurquées sur le tubercle ombilical ou simples. Région siphonale tectiforme et avec une carène siphonale entière. Cloisons, comme *Gauthiericeras* et *Peroniceras*.'

In Wiedmann's discussion, *Ciryella* was suggested as an intermediate form between *Gauthiericeras* and *Peroniceras*, with the general coiling and evolute umbilicus of the latter (U = 40 % at D = 42 mm, 51 % at D = 73 mm, and 52 % at D = 125 mm) and similar ribbing. The features recalling *Gauthiericeras* were said to be the single, entire siphonal keel.

Wiedmann gave the age of his species as Lower Coniacian, and it is based on a specimen recorded by Ciry (1940: 217). As discussed previously (p. 128), the earliest Coniacian ammonite zone recognized by Wiedmann in his 1960 paper and subsequently, that of *Tissotioides haplophyllus*, would appear to be Middle Coniacian, while Wiedmann's Zone III of *Gauthiericeras vallei*, also placed in the Lower Coniacian in 1960, is Upper Coniacian. It is suggested here that *Ciryella* is actually an Upper Coniacian form. It differs from *Gauthiericeras* only in being very evolute, yet specimens of *Gauthiericeras margae* from France have U = up to 42 %. *G. nouelianum* (d'Orbigny, 1850) has U = as little as 20 % and *G. obesum* van Hoepen, 1955, has U = up to 46,5 %. *Ciryella* thus stands in the same relationship to *Gauthiericeras* as does *Peroniceras (Peroniceras)* to the more involute *P. (Zuluiceras)*, but without the distinctive differences in ornament shown by these two subgenera. At most it is a subgenus of *Gauthiericeras*, and even this seems unnecessary.

Van Hoepen (1965) was led astray by the wide extent of intraspecific variation shown by the Zululand *Gauthiericeras*, the numbers of which by far exceed that of all other described *Gauthiericeras* collections. This led to his erection of a series of genera: *Andersonites, Hluhluweoceras, Falsebayites*, and *Fluminites*. In 1970 and 1971 low water-levels in False Bay permitted the authors to collect a range of material *in situ*, on the basis of which it is possible to demonstrate a series from very evolute individuals close to *G. roquei* (Peron, 1897) via more narrowly umbilicate forms referred to *G. obesum* van Hoepen, 1955, to narrowly umbilicate forms with rapidly expanding whorls that include Van Hoepen's *Andersonites, Falsebayites*, and *Hluhluweoceras*, the type species of which are all regarded as synonyms, the name *Gauthiericeras* ['*Andersonites*'] *listeri* van Hoepen, 1965, having priority. The type species of *Fluminites, F. albus* van Hoepen, 1965, is retained as a further species of *Gauthiericeras*, allied to a very involute species *G. albiforme* sp. nov. *Gauthiericeras libertae* van Hoepen,

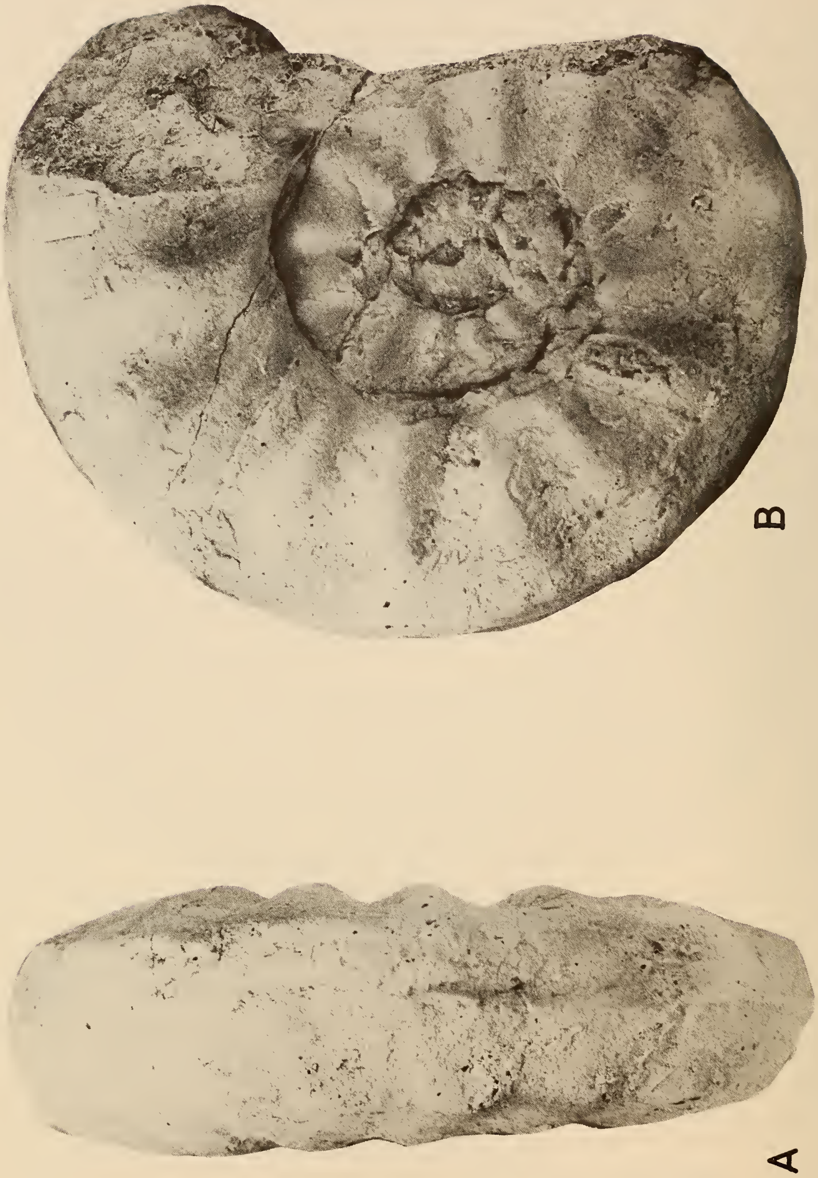

Fig. 96. *Gauthiericeras margae* (Schlüter, 1867). The specimen figured by Redtenbacher (1873, pl. 25 (fig. 1a–c)). × 1.

1955, of which *G. planatum* van Hoepen, 1955 is a synonym, is also maintained as a separate species. *Gauthiericeras* shows a number of similarities to *Prionocycloceras* Spath, 1926, and, indeed, Spath (1926: 80) considered it as transitional between *Collignoniceras* and *Gauthiericeras*. The type species differ in the strong umbilical and lateral tubercles of *Gauthiericeras margae*, and the absence of the huge spines of adult *Prionocycloceras guyabanum*. Both share a simple suture and strongly serrated keel flanked by shallow grooves but, whereas the ribs extend from the ventrolateral tubercles to the siphonal keel in *Prionocycloceras*, they decline in *Gauthiericeras*. Many *P. guyabanum* specimens have fine intercalated flank ribs.

Some species show intermediate features, but the two genera are distinct.

Prionocycloceras may well be the link between Upper Turonian *Prionocyclus* and Upper Coniacian *Gauthiericeras*. Of species referred to *Gauthiericeras* by recent workers, *G. margae peruanum* Brüggen, 1910, is a *Forresteria (Forresteria)*, as is *Gauthiericeras hoepeni* Collignon, 1965. Of Spanish species, *Gauthiericeras margae turzoi* Karrenberg, 1935, *G. margae gorda* Karrenberg, 1935, *G. vallei* Ciry, 1940, and *G. vallei gorda* Ciry, 1940, are *Prionocycloceras*.

Occurrence

Upper Coniacian of France, Spain, central Europe, north, east and west Africa, Madagascar, New Caledonia, Mexico, Colombia, and Peru. Middle Coniacian records are doubtful.

Gauthiericeras obesum van Hoepen, 1955

Figs 97–114

Gauthiericeras margae (Schlüter): Besairie, 1936: 203, pl. 24 (figs 17–18). Venzo, 1936: 104, pl. 10 (fig. 2). ? Collignon, 1965: 49, pl. 435 (fig. 1798).
Gauthiericeras obesum van Hoepen, 1955: 374, figs 25–28.

Type specimen

The holotype, by monotypy, is SAS Z12, (Figs 107–108), collected loose from the mouth of the Hluhluwe River, Zululand.

Material

SAS 85, 92/2, H200/33, H200/37, H200/76, H200/94, H200/109, SAS Z200, Z872–75, Z877, Z2015, Z2031, Z2035, BMNH C83760–C83790, and SAM–PCZ5947–50, from locality 83 locally known as Mason's Camp, Zululand, St. Lucia Formation, Coniacian IV. SAS H203/8, SAS Z12, SAM–PCZ5951 from boulder- and concretion-strewn slopes west of the St. Lucia Game Park fence, east-south-east of Hluhluwe, Zululand, St. Lucia Formation, Coniacian IV. SAS Z1055 and Z1057 from locality 73, degraded river cliffs and stream sections on north side of the Mzinene River downstream of the Munywana River, Zululand, St. Lucia Formation, Coniacian IV. SAS A1510 and BMNH C83801–C83806 from locality 22, on the north side of the Nyalazi River near Nyalazi River Trading Store, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
A1754	98,0	35,0(35,7)	37,0(37,7)	0,95	38,0(38,8)	—:17
H200/76	81,0	27,0(33,3)	31,0(38,3)	0,87	31,0(38,3)	—:—
PCZ–5948	85,0	27,0(31,8)	30,0(35,3)	0,90	35,0(41,2)	18:18
H200/34	108,0	36,0(33,3)	40,0(37,0)	0,90	40,0(37,0)	—:—
PCZ5497	108,0	37,0(34,2)	42,0(38,9)	0,88	41,0(40,0)	—:17
PCZ5949	108,0	38,0(35,2)	39,0(36,1)	0,97	43,0(39,8)	10×2:10×2
Z200	123,0	45,0(36,6)	50,0(40,6)	0,90	48,0(39,0)	—:20
SAS–85	124,0	—	47,0(37,9)	—	48,0(38,9)	—:16
Z1055	127,0	40,0(31,5)	46,0(36,2)	0,87	53,0(41,7)	20:20
Z473	129,0	44,0(34,1)	47,0(36,4)	0,94	53,0(41,1)	17:—
H203/8	130,0	41,0(31,5)	47,0(36,1)	0,87	57,0(43,8)	18:18
H200/33	134,0	45,0(33,6)	48,0(35,8)	0,94	53,0(39,6)	—:—
Z1057	134,0	39,0(29,1)	45,0(33,6)	0,87	52,0(38,8)	21:21
Z873	140,0	48,0(35,0)	52,0(37,1)	0,92	52,0(37,1)	19:19
Z191	150,0	4,0(29,3)	51,0(34,0)	0,86	64,0(42,7)	16:—
Z12	150,0	52,0(34,7)	57,0(38,0)	0,91	59,0(39,3)	18:18
H200/94	164,0	—	61,0(37,2)	—	61,0(37,2)	17:18
Z2021	167,0	54,0(32,3)	58,0(34,7)	0,93	69,0(41,3)	—:—
Z872	167,0	55,0(32,9)	59,0(35,3)	0,93	67,0(40,1)	23:23
PCZ5950	185,0	59,0(31,9)	66,0(35,7)	0,82	76,0(41,1)	20:20
Z2035	190,0	58,0(30,5)	67,0(35,3)	0,87	82,0(43,2)	19:19
Z874	204,0	60,0(29,4)	71,0(34,8)	0,84	91,0(44,6)	21:21
92/2	221,0	—	71,0(32,1)	—	101,0(45,7)	—:—
Z2030	225,0	65,0(28,9)	74,0(32,9)	0,88	98,0(43,6)	18:18
92	235,0	70,0(29,8)	80,0(34,0)	0,87	103,0(43,8)	21:21
H200/109	237,0	73,0(30,8)	85,0(35,9)	0,86	100,0(42,2)	17:17
Z2015	245,0	72,0(29,4)	80,0(32,5)	0,90	106,0(43,3)	17:17
Z877	285,0	75,0(26,3)	90,0(31,6)	0,83	136,0(43,7)	19:19
PCZ5951	308,0	83,0(26,9)	101,0(32,8)	0,82	141,0(45,8)	18:18
Z875	311,0	83,0(26,7)	98,0(31,5)	0,85	144,0(46,3)	—:—

Description

The umbilical width of the species varies between 37 and 46 per cent of the total diameter, but the majority of specimens have umbilical widths of 39 to 44 per cent (Fig. 97). Coiling is very evolute and the whorls are only slightly overlapping, so that the dorsal zone of impression is very shallow. It appears that the more widely umbilicate specimens grew to a larger size than the more narrowly umbilicate ones, but this may possibly be only an artefact of preservation rather than an indication of dimorphism. The whorl section is compressed throughout, Wb/Wh ratios ranging from 0,82 to 0,97.

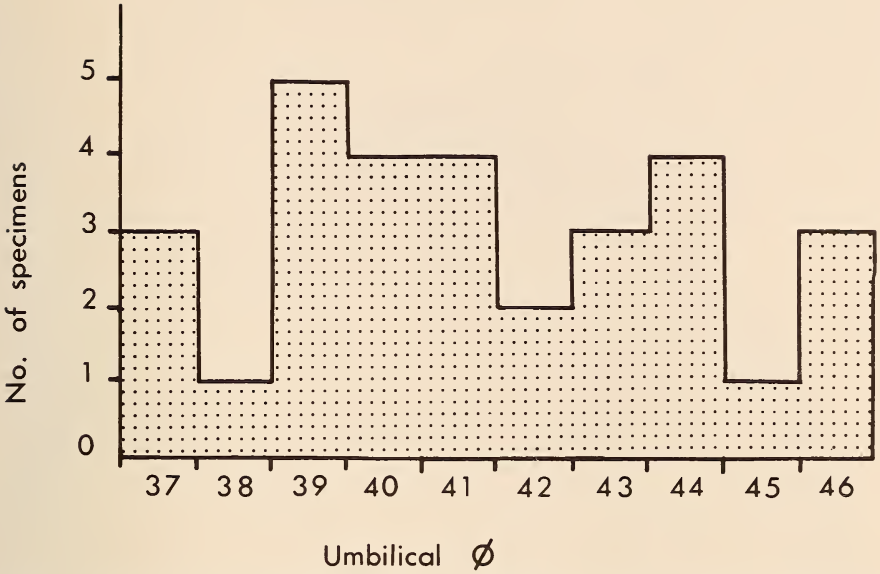

Fig. 97. Histogram illustrating distribution of umbilical width in Zululand population of *Gauthiericeras obesum* van Hoepen, 1955.

Density of ribbing in the population is reasonably constant, varying between 16 and 23 per whorl, but the majority of specimens have a rib density of 17 to 18 per whorl. Strength of ornament is variable, but this depends to some extent on preservation, and is often accentuated through abnormal thickening of the shell as a result of diagenetic growth of calcite. Specimen SAS Z473 (Fig. 98) has much of the inner whorls preserved. Here ornament consists of radial to slightly rursiradiate, very strong ribs, apparently all single, each bearing two rows of tubercles. The umbilical ones are pinched bullate, protruding far beyond the level of the ribs, especially in places where the shell has been thickened diagenetically. The ventrolateral tubercles are clavate and pointed, and lean against and impress into the umbilical wall of the succeeding whorl. On the outer whorls, the ventrolateral tubercles become weaker and rounded clavate, whereas the umbilical tubercles remain prominently bullate and merge into the ribs.

Differences in strength of ornament in the adult stage become obvious when comparing specimens SAS Z869 (Fig. 99) and SAS Z2030 (Fig. 100), the latter with strong ribbing and tuberculation, and the former with virtually smooth flanks.

Some specimens retain the body chamber (e.g. SAM–PCZ5951) (Figs 101–102), consisting of about three-quarters of a whorl. Here ribbing becomes bolder and wider spaced. The umbilical bullae may disappear completely, fusing with the rib. The ribs may also curve gently forward or become slightly sinuous.

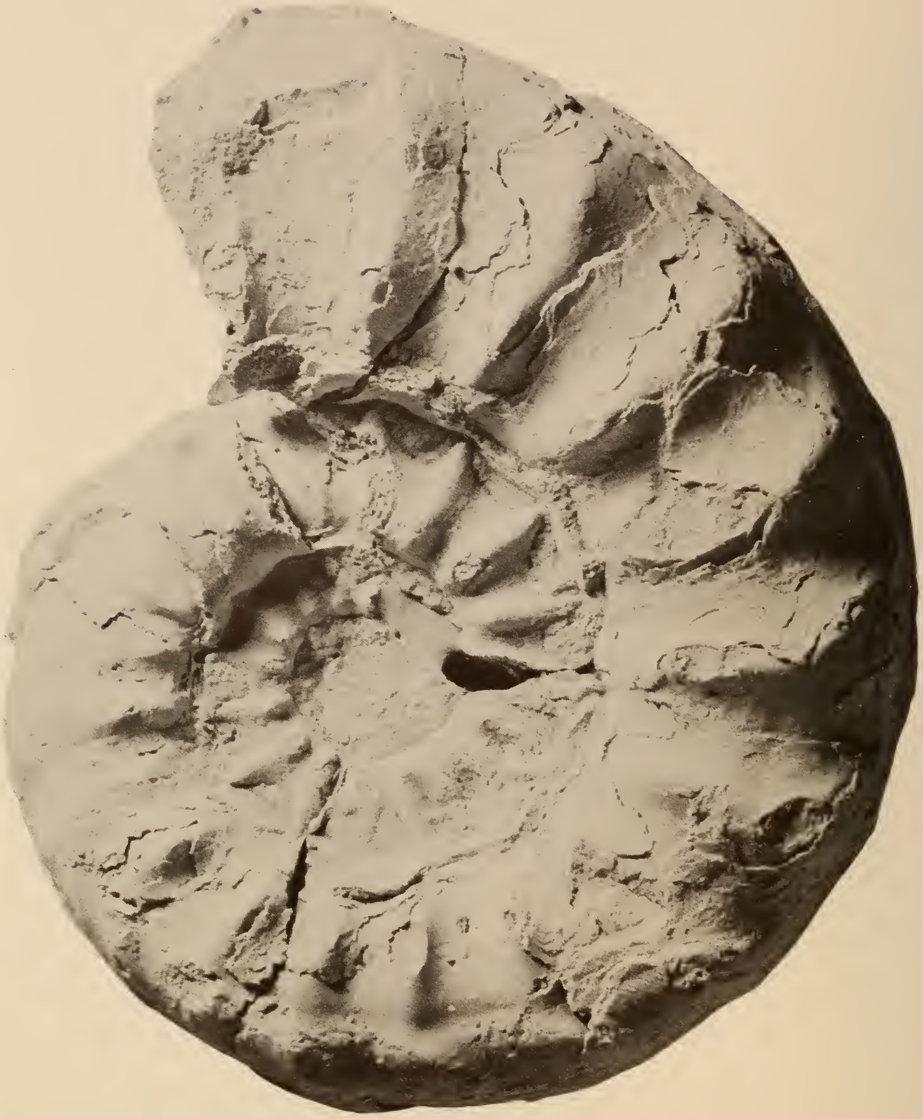

Fig. 98. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z473. Specimen with part of inner whorls preserved, showing early strong ornament. × 1.

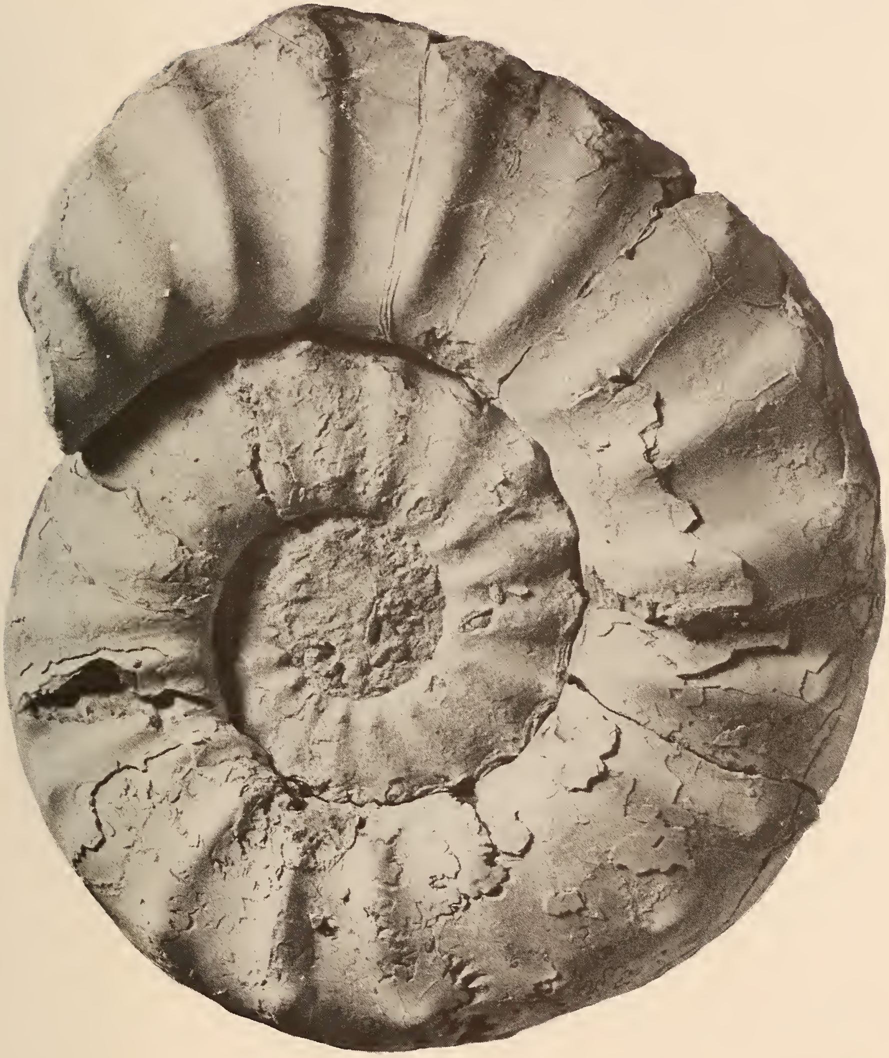

Fig. 99. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z869. Specimen with weak ornament compared to Figure 100. × 0,67.

A very large body chamber fragment, NMB D1060 (Fig. 103), with two strong ribs but distinct umbilical and ventrolateral tubercles, may belong here or perhaps to *G. listeri* described below.

The suture lines are very simple as shown in Figures 99–100, and 105.

Discussion

Gauthiericeras obesum most closely resembles the type species, *G. margae* (Schlüter, 1867). Schlüter's figure is highly idealized, and a cast of the basis of Schlüter's figure is shown in Figures 20C and 94–95. The outer whorl is crushed almost flat and the inner whorls survive only as an external mould. A topotype specimen, also in Schlüter's collection, the specimen figured by Redtenbacher (1873: 109, pl. 25 (fig. 1a—c)) from the Gosau Beds of Austria, De Grossouvre's material (1894: 90, pl. 15 (figs 1–2)) (see Fig. 96 herein), plus new material from Touraine show that *G. margae* differs from *G. obesum* in several respects. The ribs commonly arise from bullae in pairs in juveniles, a feature not seen in *G. obesum*; there is a lateral tubercle from which the ribs also branch, and the siphonal keel is strongly serrated. Adults are more closely comparable but, whereas the umbilical bullae perch on the umbilical shoulder in *G. obesum*, they migrate outward to an inner flank position in *G. margae.*

G. nouelianum (d'Orbigny, 1850) has been illustrated by Sornay (1955); it is much more involute than *G. obesum* (U = 20–27,5 %; see Kennedy in press for details). It co-occurs with *G. margae* and, like that species, has branching ribs, lateral tubercles, and a serrated keel, all of which render it easily separable from *G. obesum*. *G? boreaui* (de Grossouvre) (1894: 111, pl. 7 (fig. 3)) is a diminutive species, involute, feebly and flexuously ribbed, and lacks ventrolateral tubercles.

Gauthiericeras roquei Peron, 1897: 52, pl. 8 (fig. 1), pl. 9 (figs 1–2), pl. 17 (fig. 6)) (Fig. 115 herein) is a very evolute species (U = 43–44 %). Ornament is very distant, with only ten ribs on the outer whorl compared with nearly double that number in similarly evolute *G. obesum*.

Gauthiericeras listeri (van Hoepen, 1965), of which *Hluhluweoceras fugitivum* van Hoepen, 1965, *Falsebayites peregrinus* van Hoepen, 1965, and *Gauthiericeras listeriforme* Collignon, 1965, are synonyms, is a contemporary of *G. obesum*. It differs in being more involute (U = 32–36 %) with a compressed whorl section in most specimens. It stands in the same relationship to *G. obesum* as does *G? nouelianum* to *G. margae*. These involute and evolute forms may be dimorphs, but this cannot be proven.

Occurrence

Coniacian IV of Zululand. Upper Coniacian *Gauthiericeras margae* and *Prionocycloceras guyabanum* Zone of Madagascar.

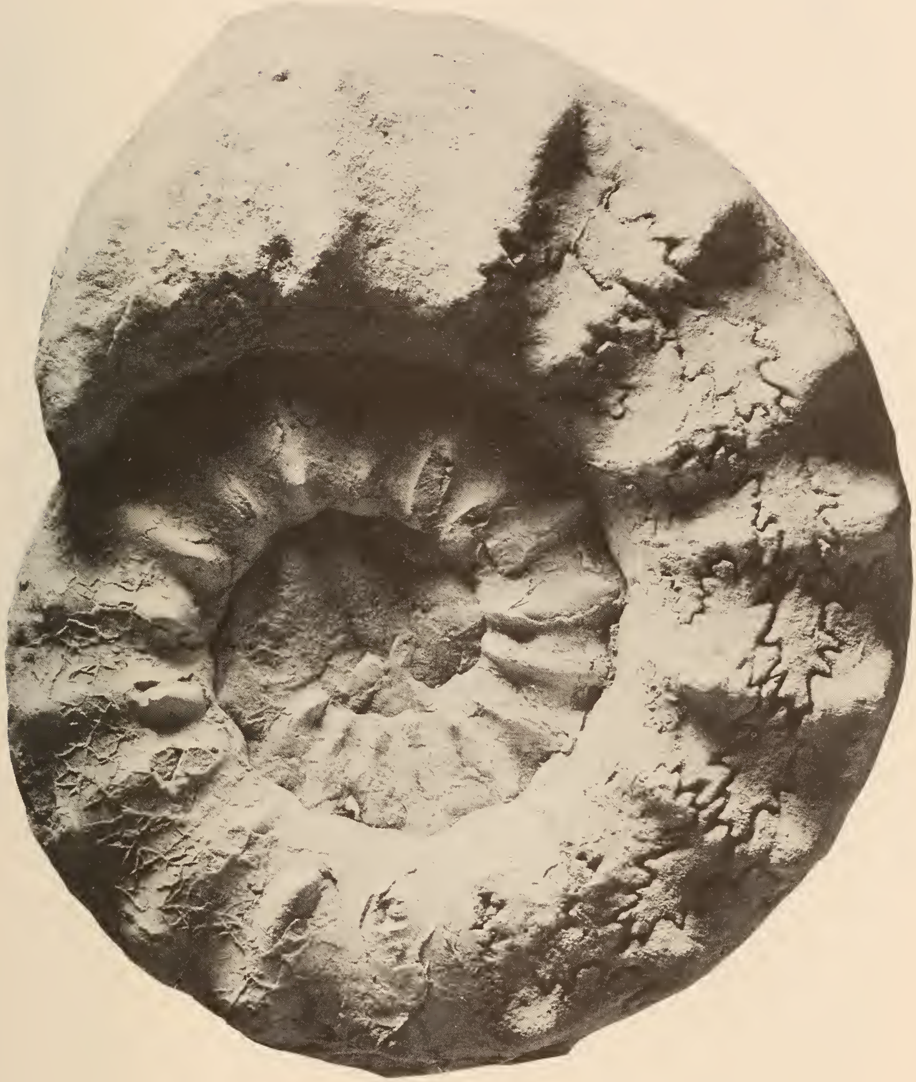

Fig. 100. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z2030. Specimen with strong ornament compared to Figure 99. × 0,63

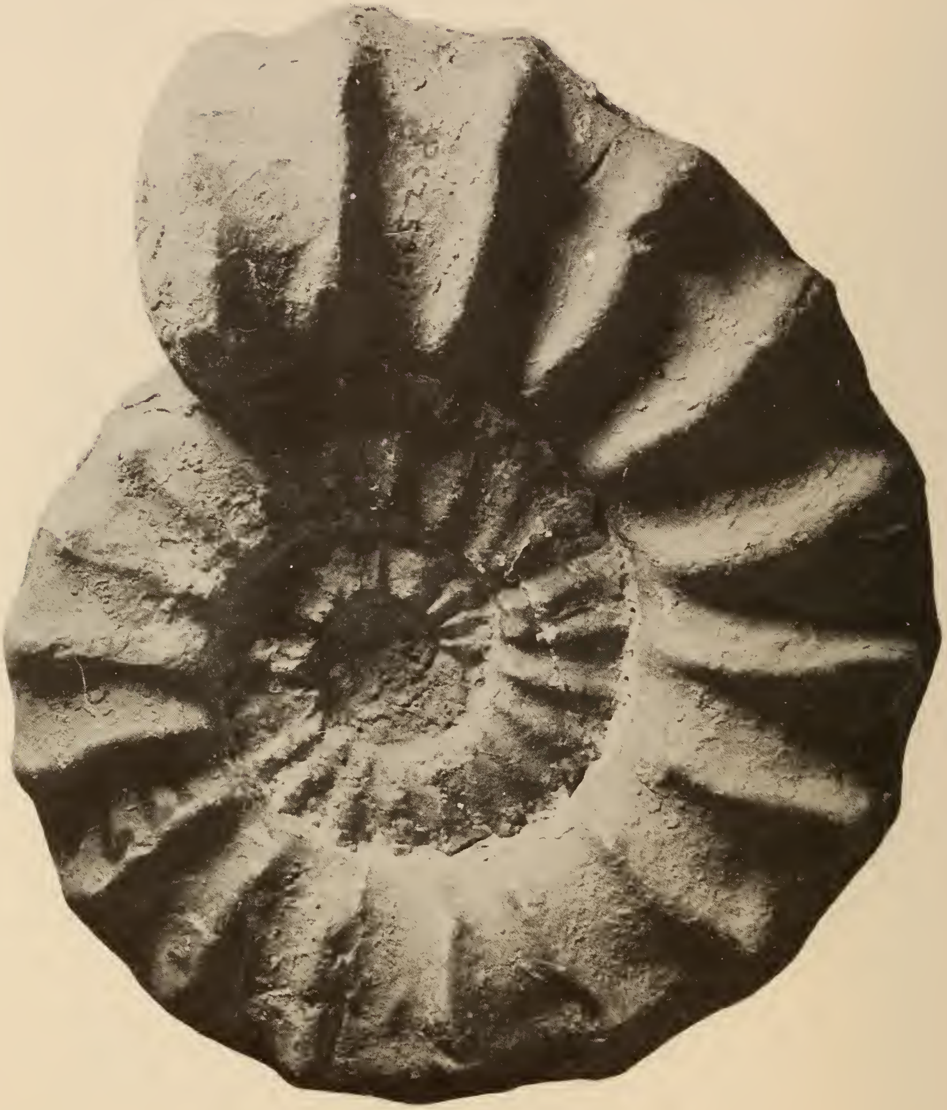

Fig. 101. *Gauthiericeras obesum* van Hoepen, 1955. SAM–PCZ5951. Large, evolute specimen with body chamber up to three-quarters of a whorl in length. × 0,48.

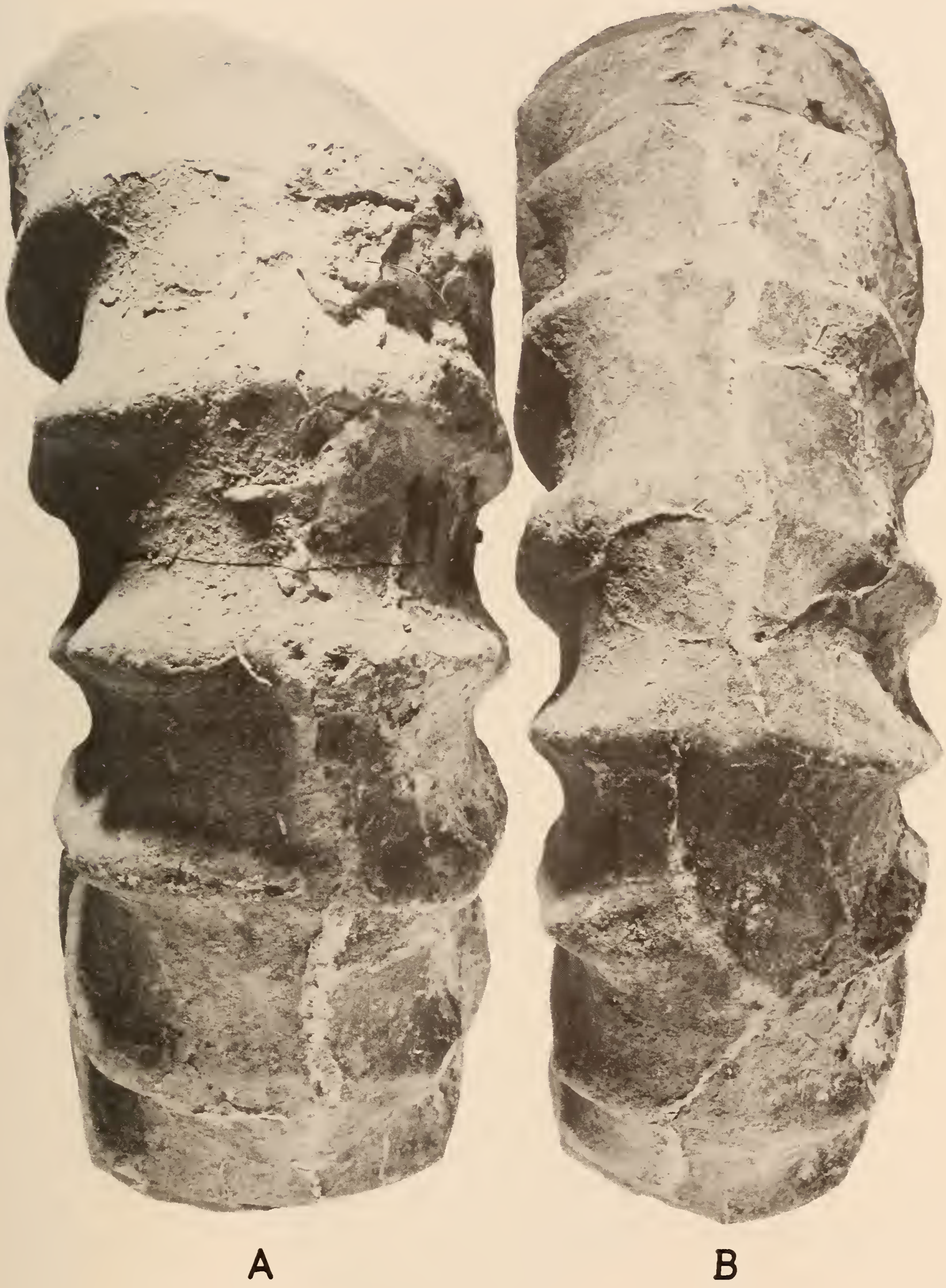

Fig. 102. *Gauthiericeras obesum* van Hoepen, 1955. SAM–PCZ5951, dorsal views of two sections of the body chamber. × 0,6

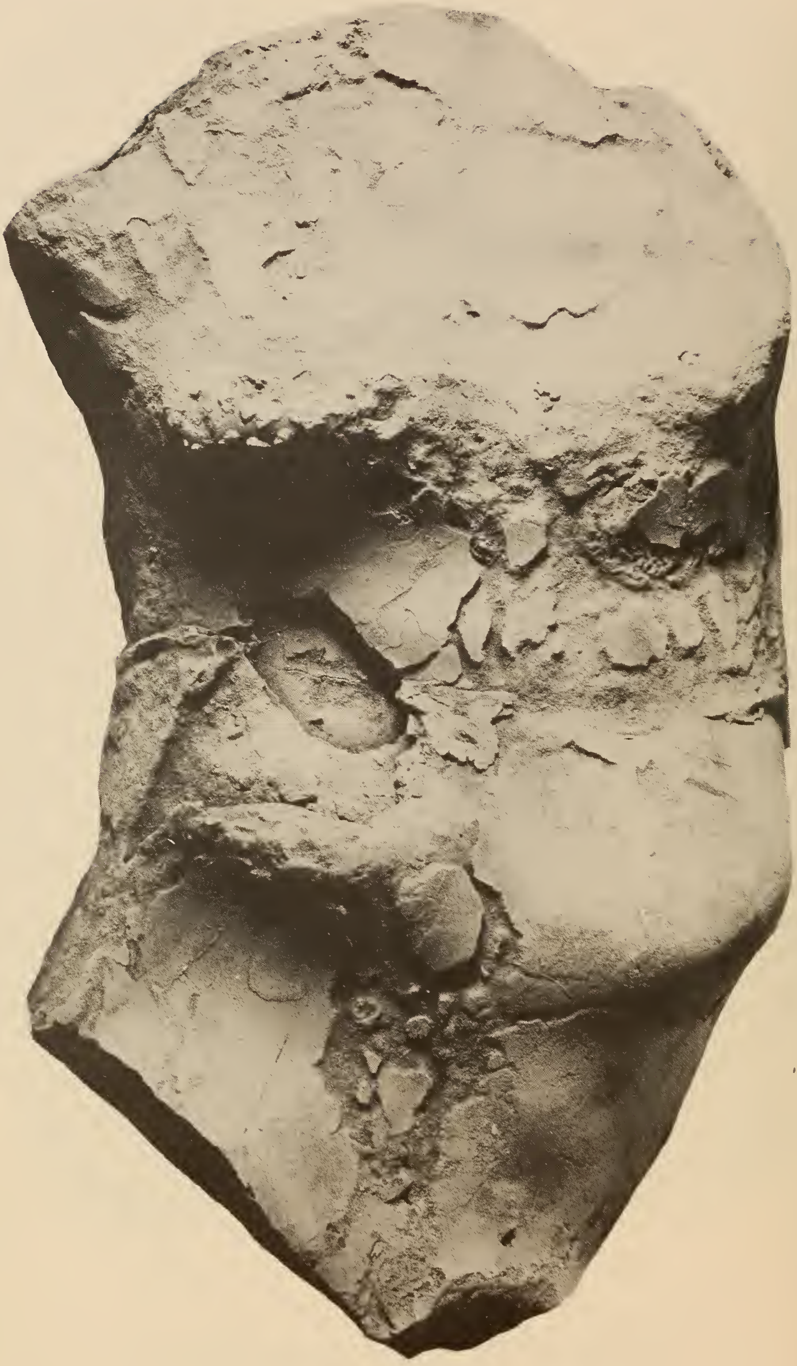

Fig. 103. *?Gauthiericeras obesum* van Hoepen, 1955. NMB D1060, large body chamber fragment. × 0,72.

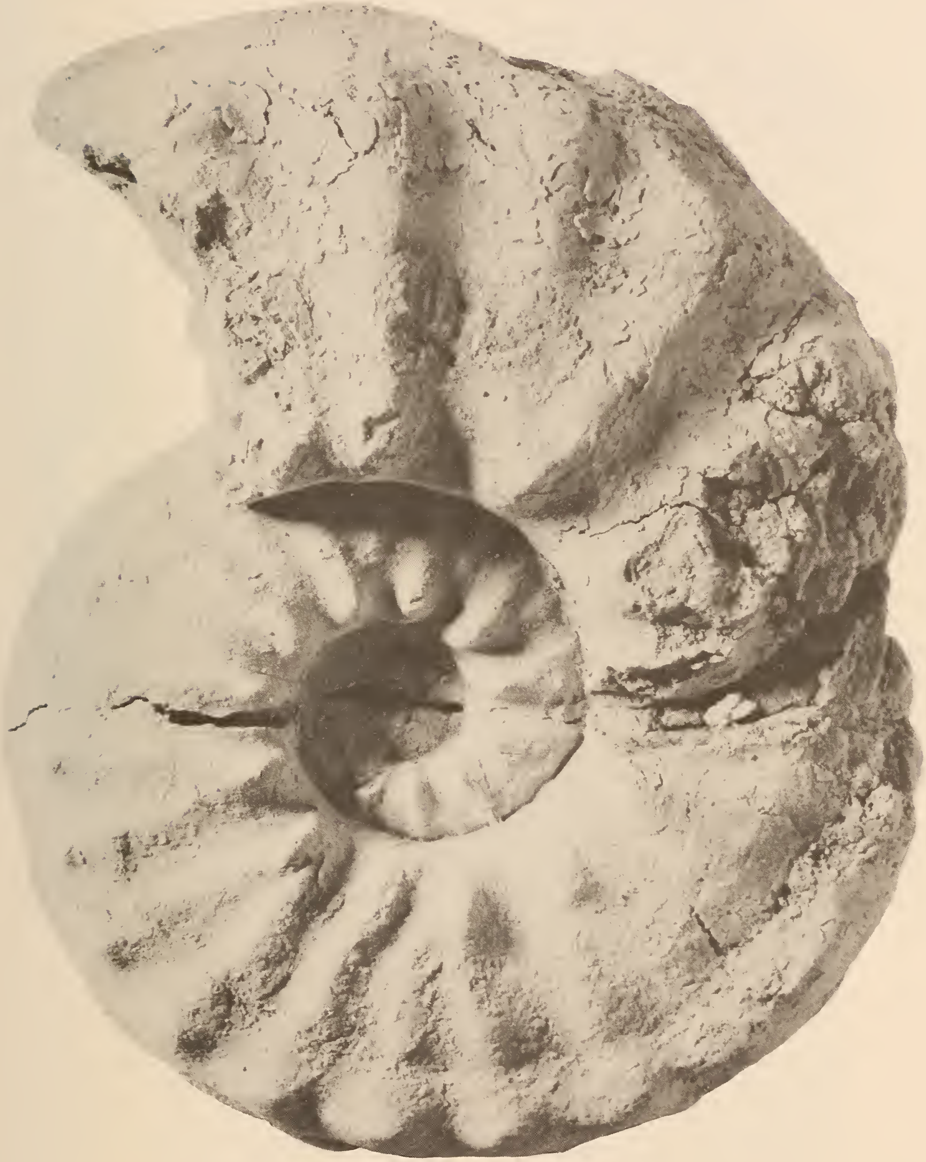

Fig. 104. *Gauthiericeras obesum* van Hoepen, 1955. SAS A1510. Individual differing from most Zululand specimens in showing numerous rib bifurcations. × 0,82.

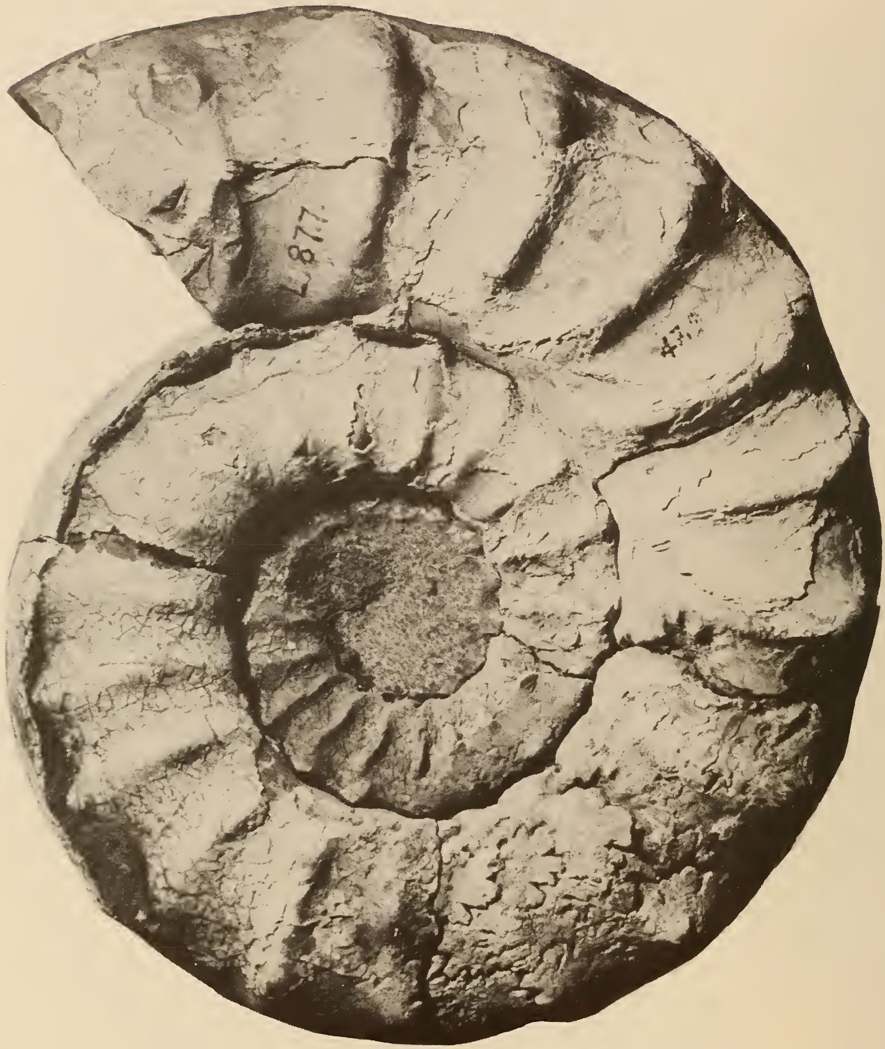

Fig. 105. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z877, large specimen with wide umbilicus. × 0,5.

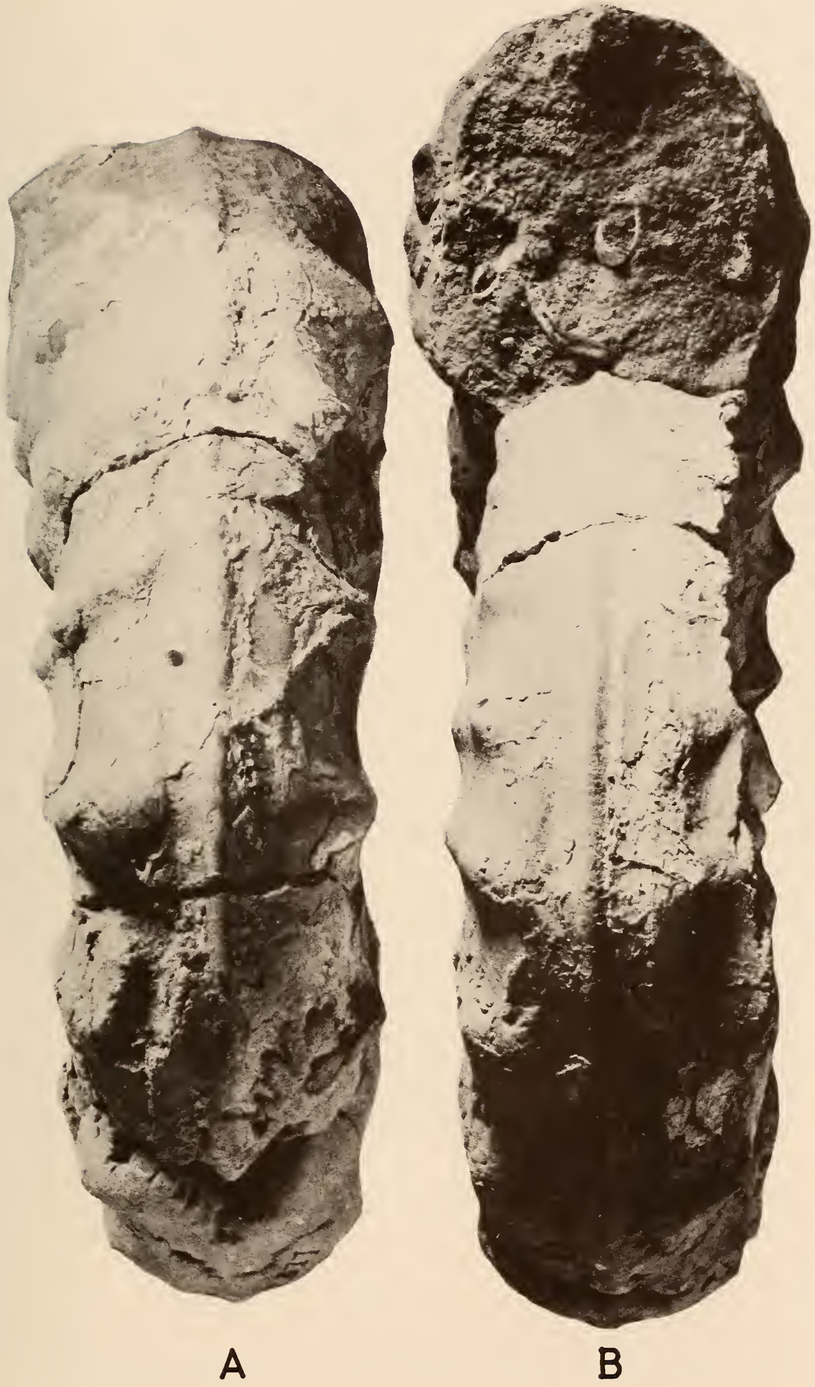

Fig. 106. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z877, large specimen with wide umbilicus. × 0,61.

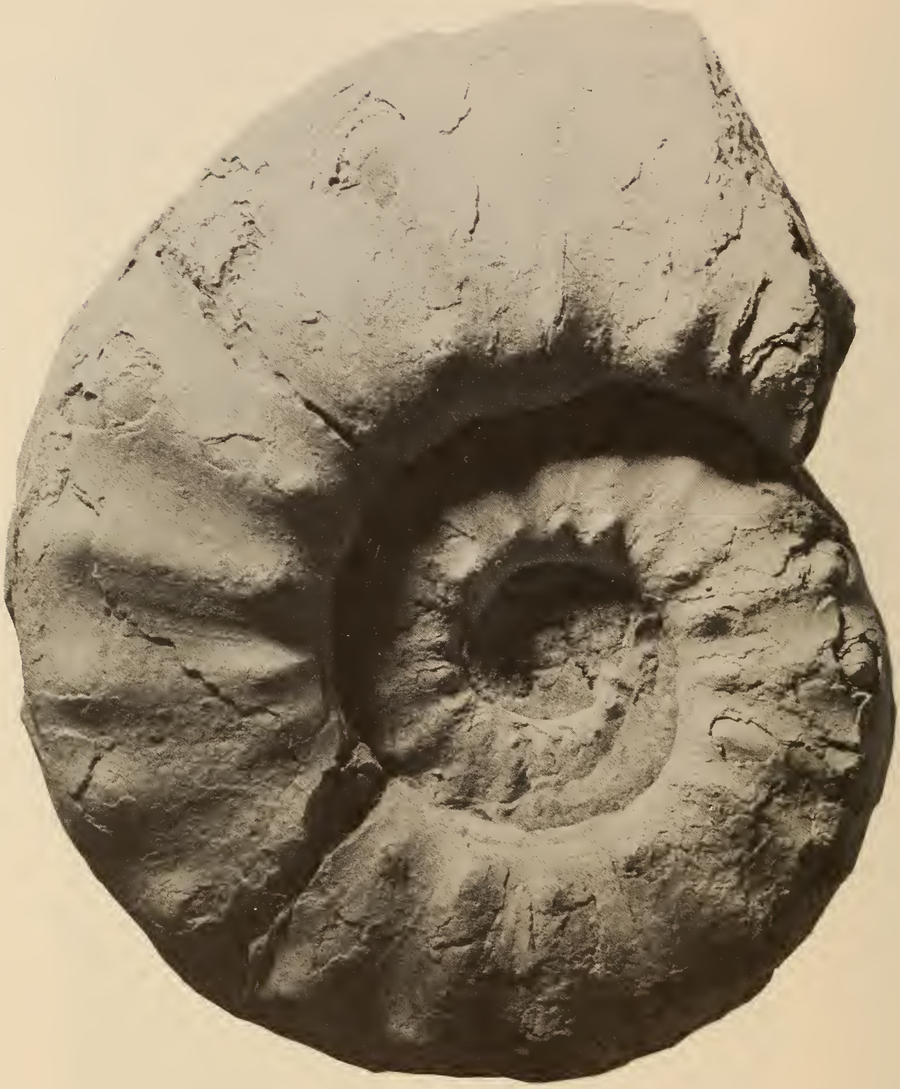

Fig. 107. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z12, the holotype. × 0,8.

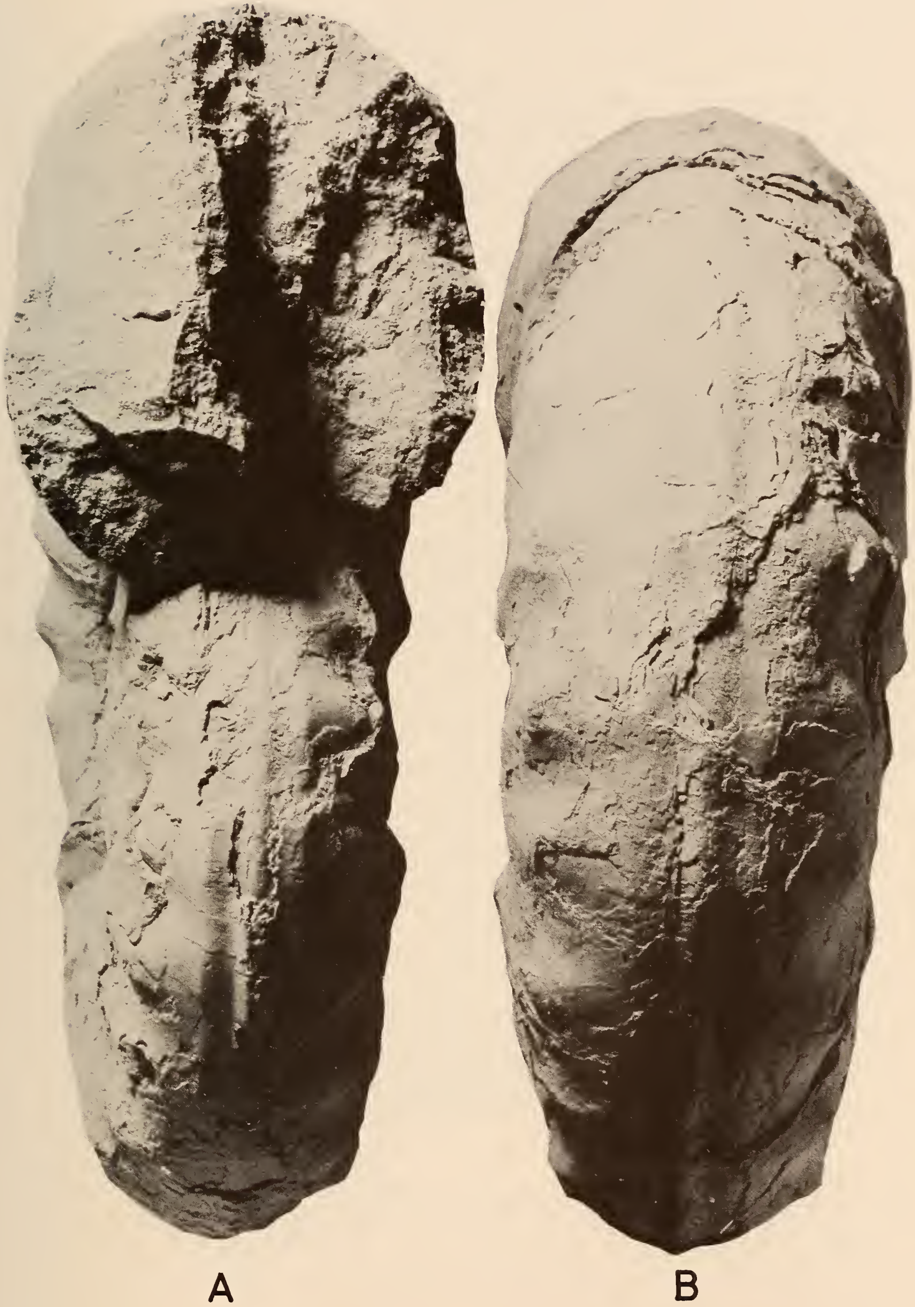

Fig. 108. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z12, the holotype. × 1.

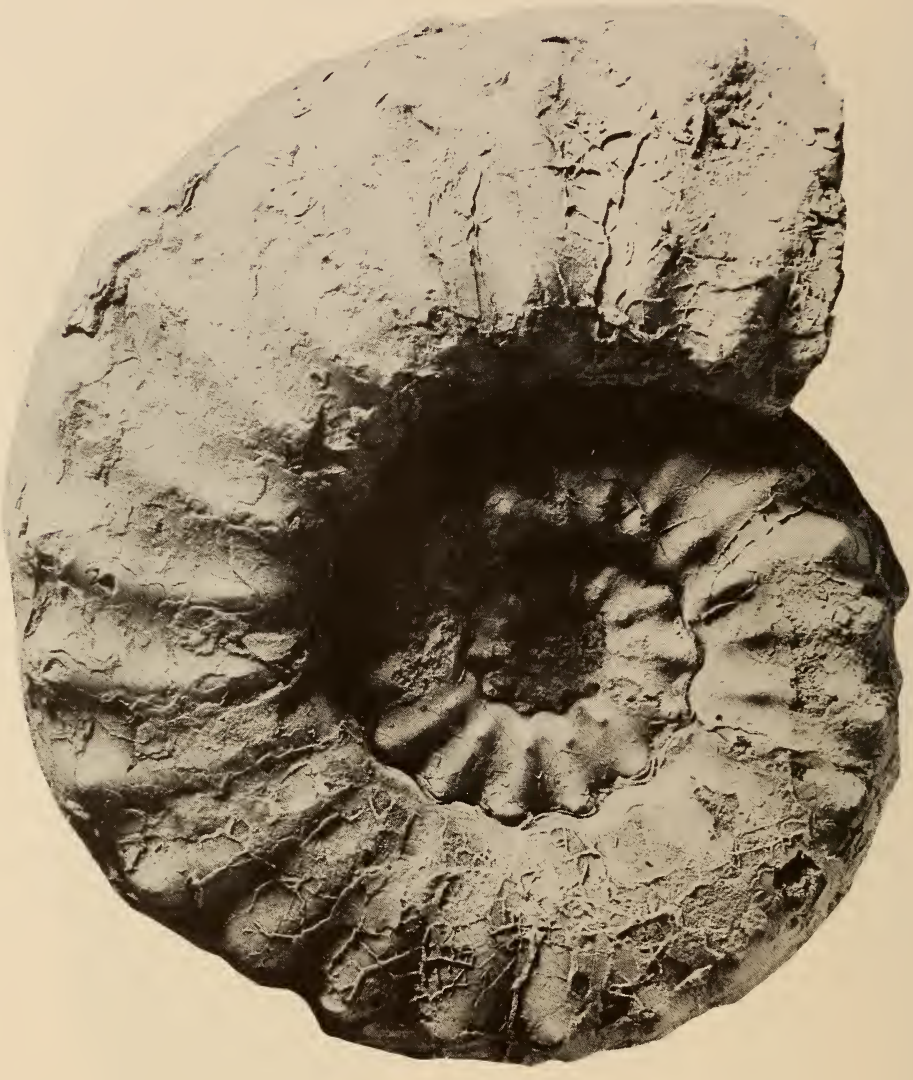

Fig. 109. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z872. × 0,88.

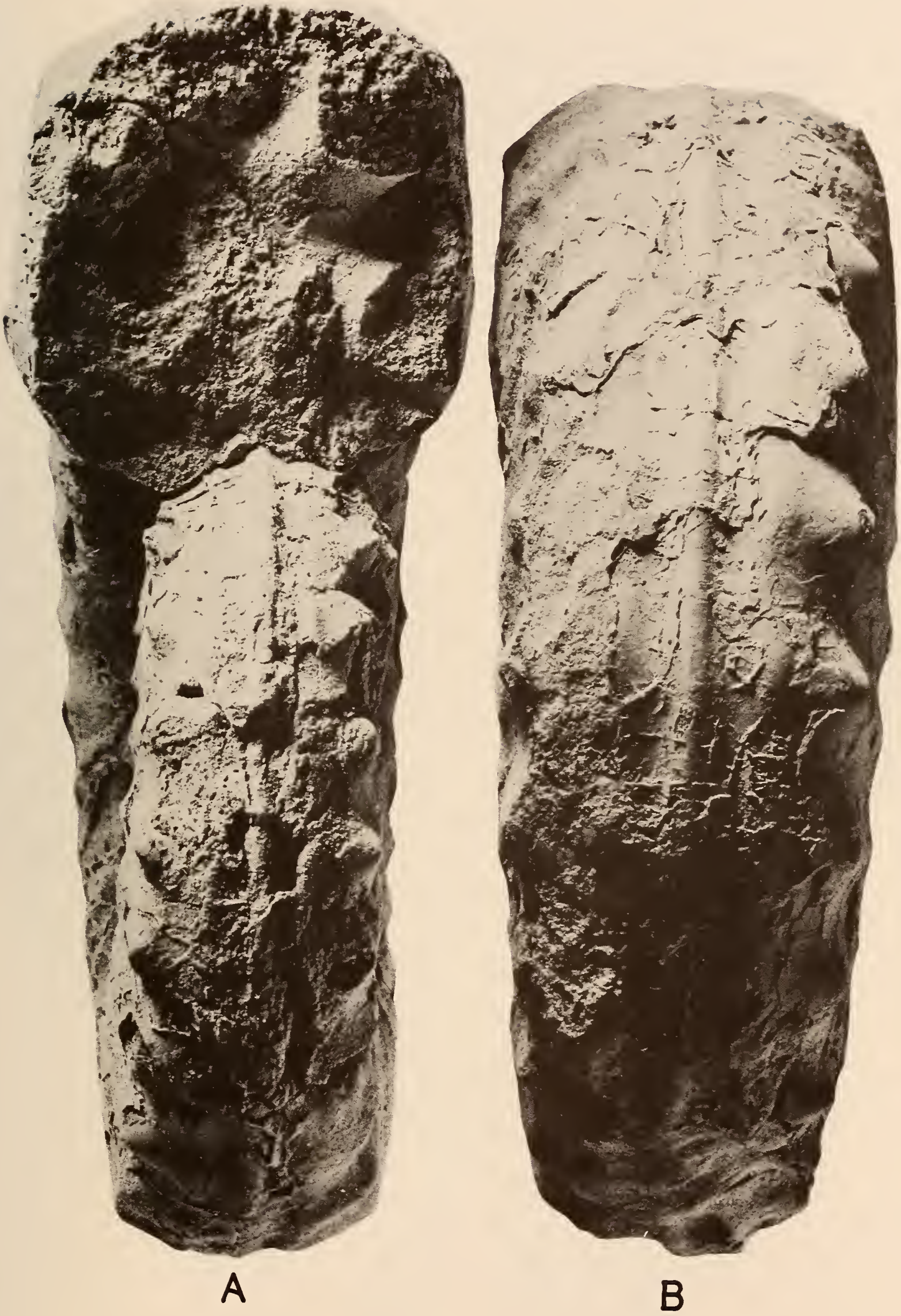

Fig. 110. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z872. × 1.

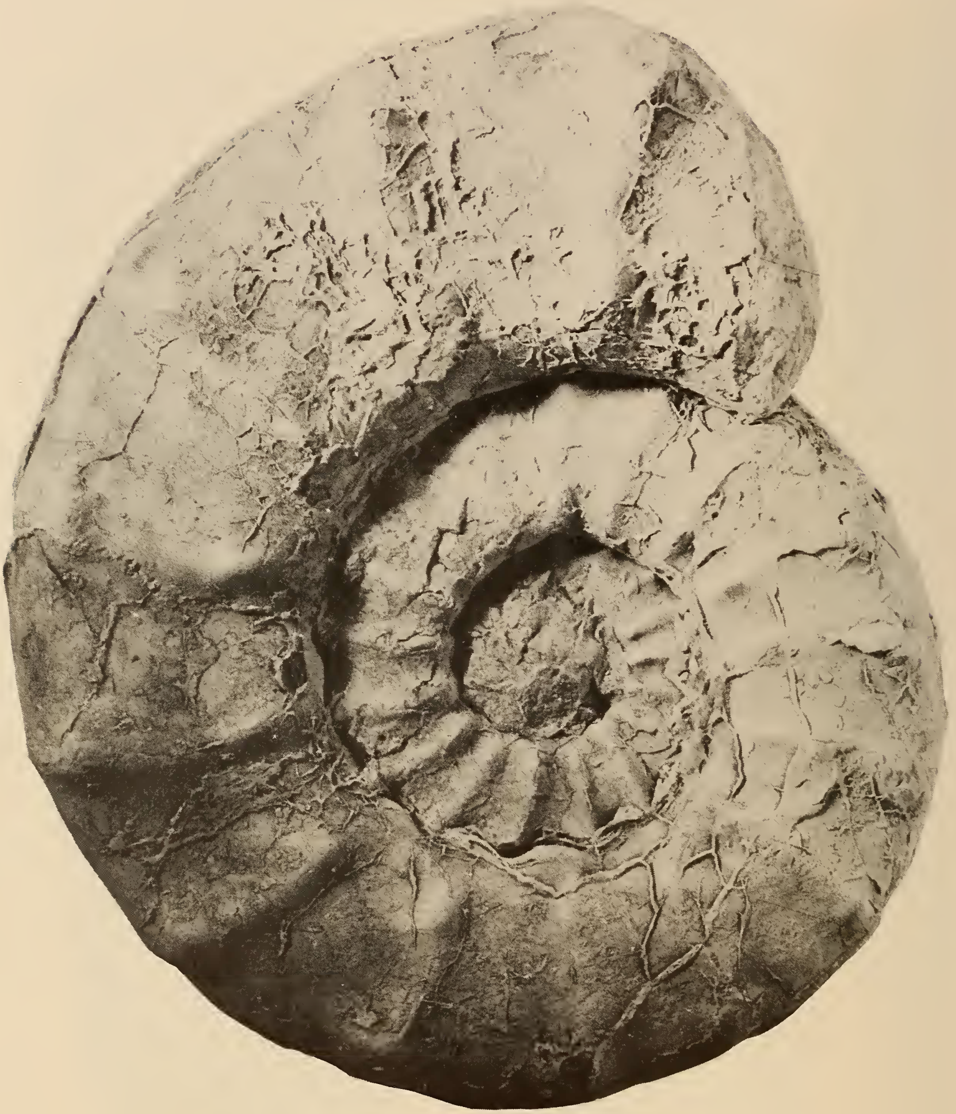

Fig. 111. *Gauthiericeras obesum* van Hoepen, 1955. SAS Z2015. × 0,6.

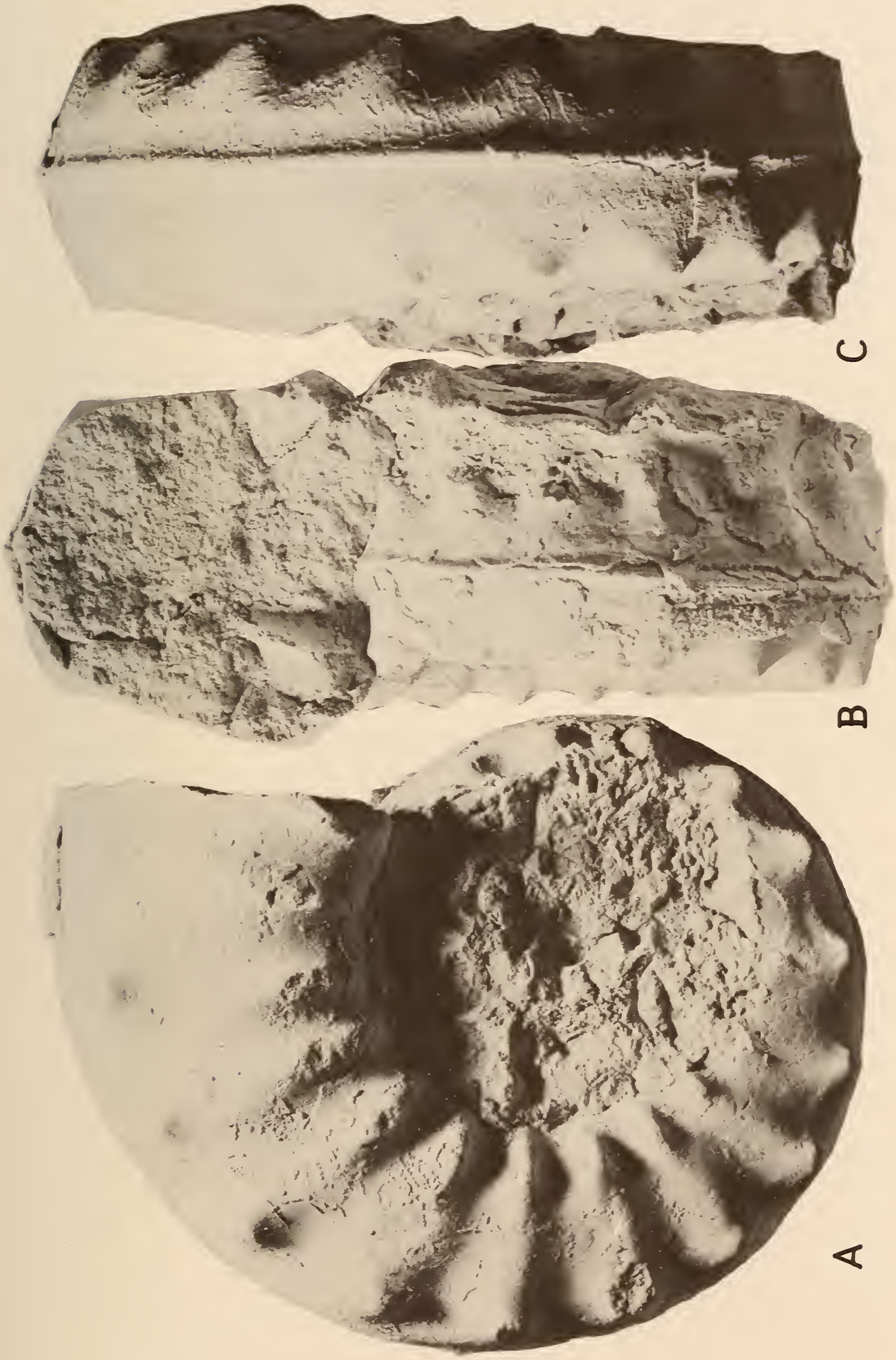

Fig. 112. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5497. × 1.

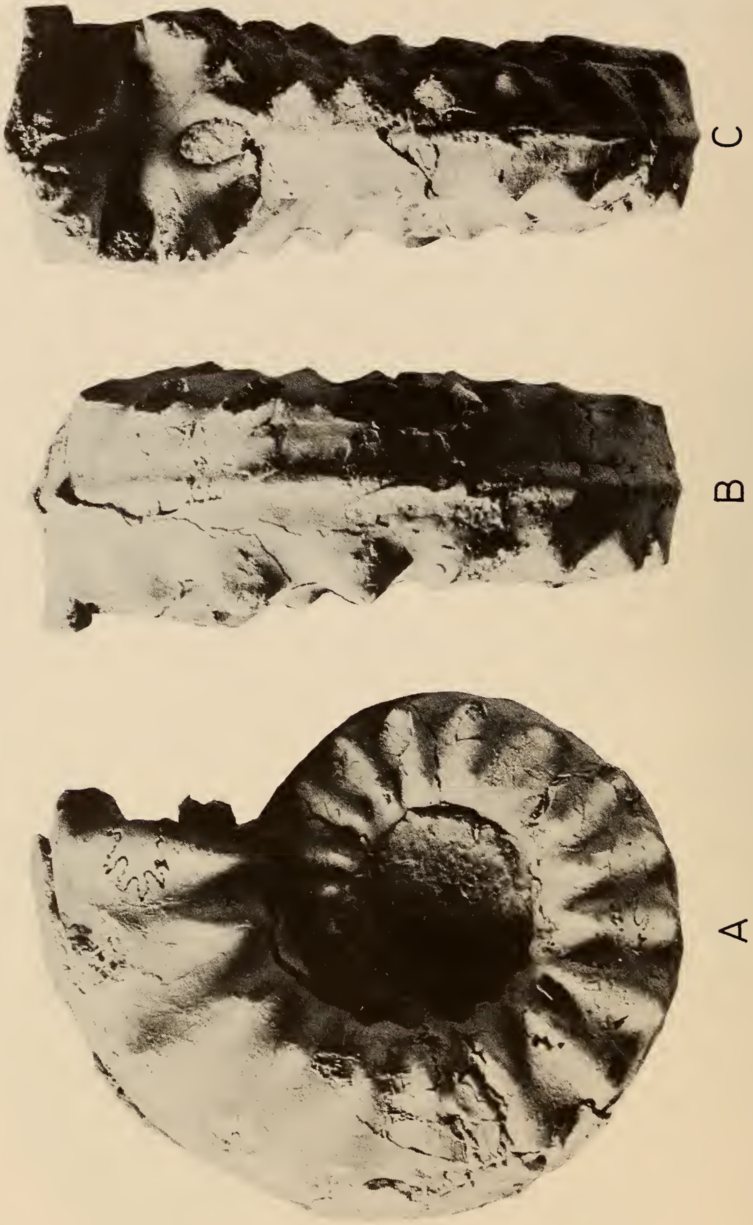

Fig. 113. *Gauthiericeras obesum* van Hoepen, 1955. SAM-PCZ5948. × 1.

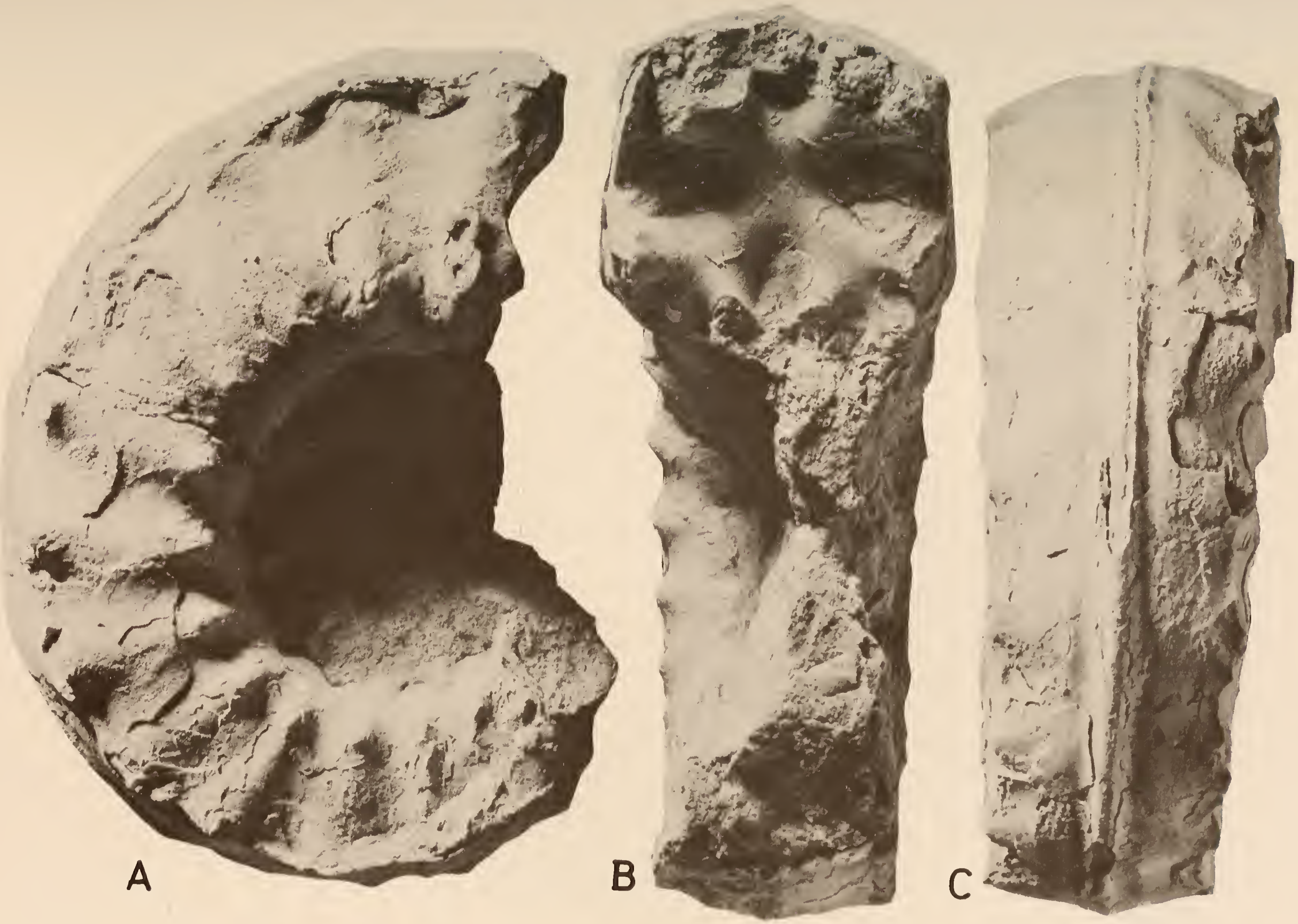

Fig. 114. *Gauthiericeras obesum* van Hoepen, 1955. SAM–PCZ5940. × 1.

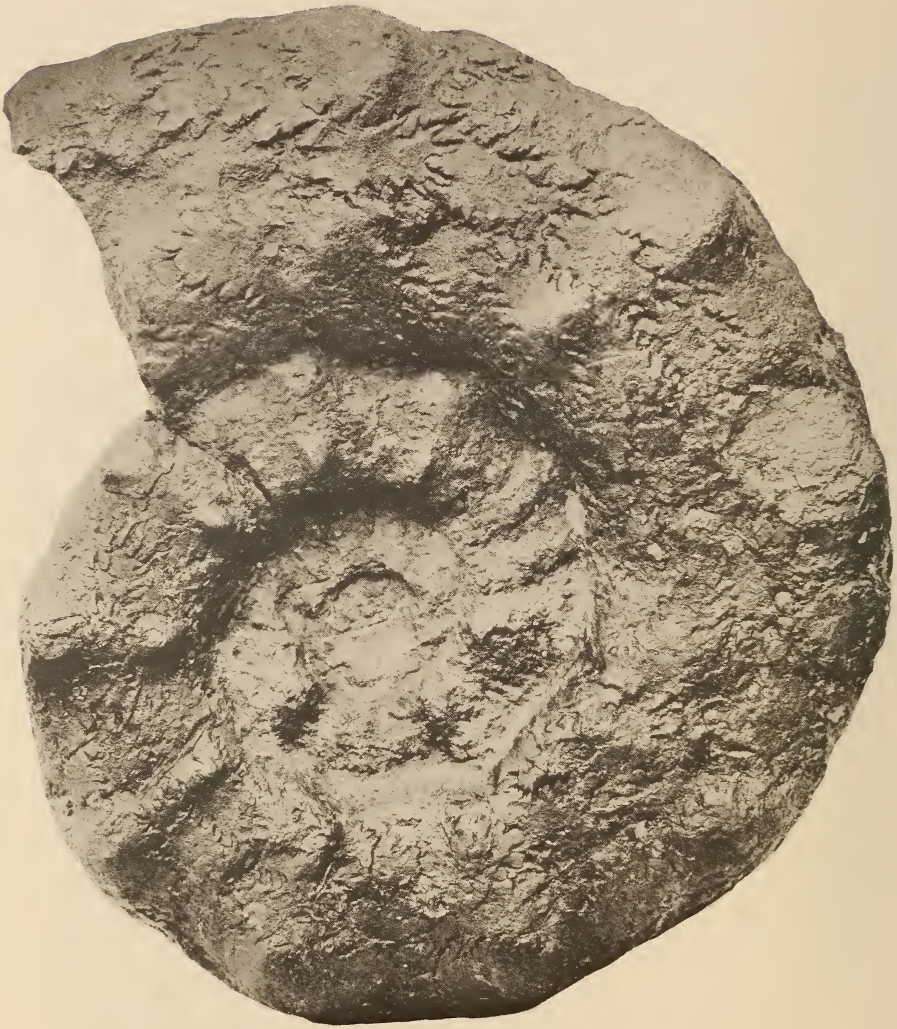

Fig. 115. *Gauthiericeras roquei* Peron. (After Peron, 1896, pl. 8 (fig. 1). Reduced.)

Gauthiericeras listeri (van Hoepen, 1965)

Figs 116–123

Andersonites listeri van Hoepen, 1965: 31, pl. 23, text-fig. 8b, d.
Hluhluweoceras fugitivum van Hoepen, 1965: 33, pl. 25, text-fig. 8a, c.
Falsebayites peregrinus van Hoepen, 1965: 34, pl 26. text-fig. 9f–g.
Gauthiericeras listeriforme Collignon, 1965: 49, pl. 435 (fig. 1797).

Type specimens

The holotype, by original designation, is SAS Z754 (Figs 116–117B), from locality 91, degraded river cliffs and artificial cut west of the boundary fence of St. Lucia Game Reserve, east-south-east of Hluhluwe, Zululand. This area is strewn with rubble derived from the St. Lucia Formation, Coniacian IV and V, and the precise horizon cannot be stated. The holotype of *Hluhluweoceras fugitivum* is SAS Z755, from the same horizon as the holotype of *Gauthiericeras listeri*. The holotype of *Falsebayites peregrinus* is SAS Z341, the paratype is SAS Z339, both from a little to the north of the previous site. Their precise horizon is similarly uncertain.

Material

SAS H206/2, a topotype, was also collected loose; SAS Z342 is from 'close by'. BMNH C83791 is from locality 83, where it is firmly dated as Coniacian IV.

Dimensions

	D	*Wb*	*Wh*	*Wb*/*Wh*	*U*	*R*
H206/2	119,0	42,0(35,3)	48,0(40,3)	0,87	43,0(36,1)	18:19
Z755	180,0	65,0(36,1)	71,0(39,4)	0,91	64,0(35,6)	—
Z341	*c.*190,0	*c.*68,0(35,8)	*c.*72,0(37,9)	*c.*0,94	*c.*65,0(34,2)	—
Z754	195,0	74,0(37,9)	73,0(37,4)	1,01	70,0(35,9)	—
G. listeriforme (after Collignon)						
	102,0	47,0(46,0)	42,0(41,2)	1,12	35,0(34,3)	9:10

Description

The whorls expand rapidly and the umbilicus is narrow, comprising 32 to 36 per cent of the total diameter. The whorl section is compressed in the majority of specimens but may become slightly depressed on the later septate whorls. The umbilical wall is generally rounded, the flanks are very little inflated, and the venter is broadly rounded.

Only one specimen has the inner whorls preserved (SAS H206/2 Fig. 122). The ventrolateral tubercles are concealed in the umbilical seam and the umbilical tubercles are displaced somewhat up the flanks, as in *G. margae*. They are conical to radially elongated, but very irregularly developed. Intercalatory ribs, which do not bear umbilical tubercles, sometimes occur.

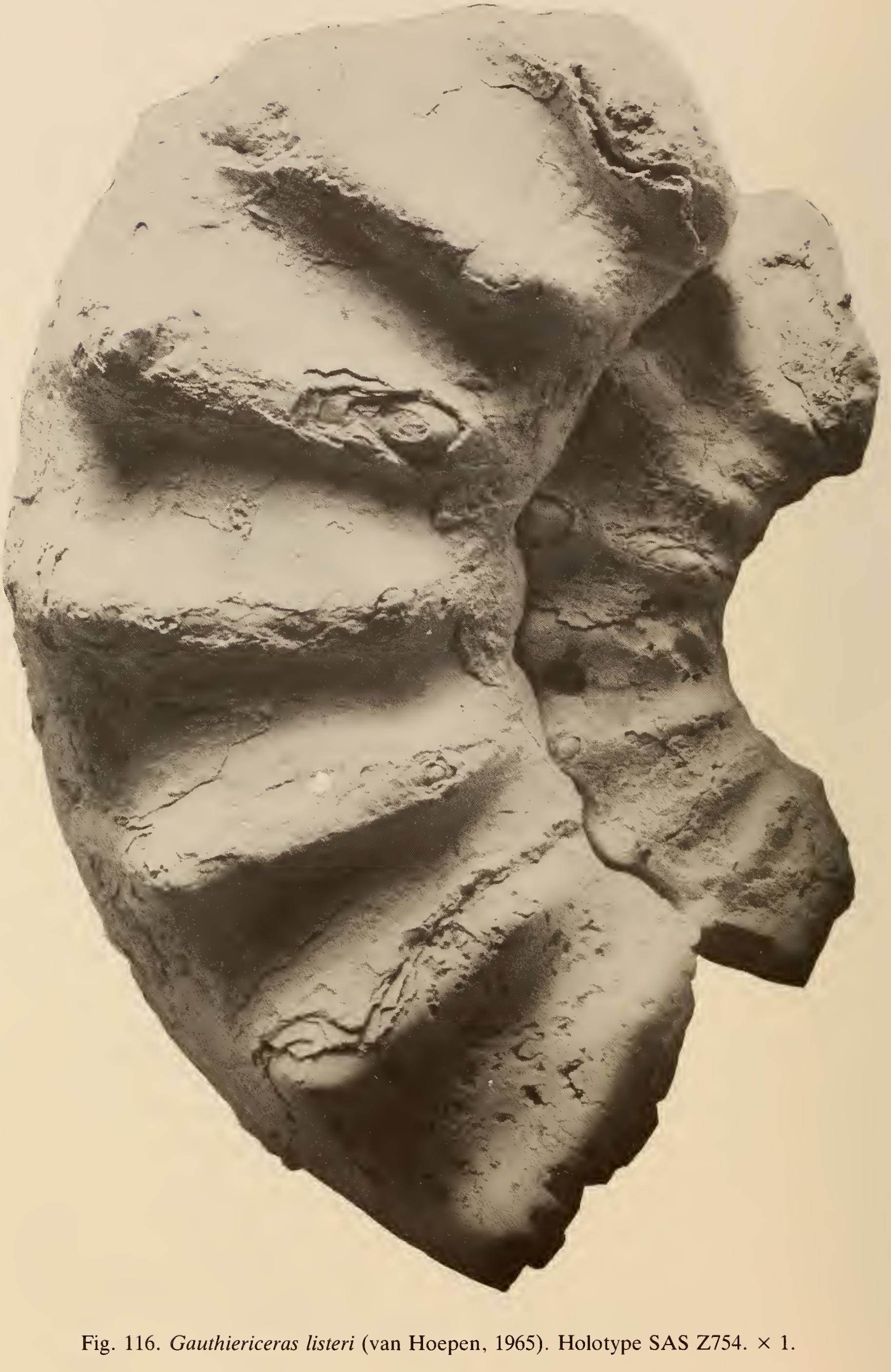

Fig. 116. *Gauthiericeras listeri* (van Hoepen, 1965). Holotype SAS Z754. × 1.

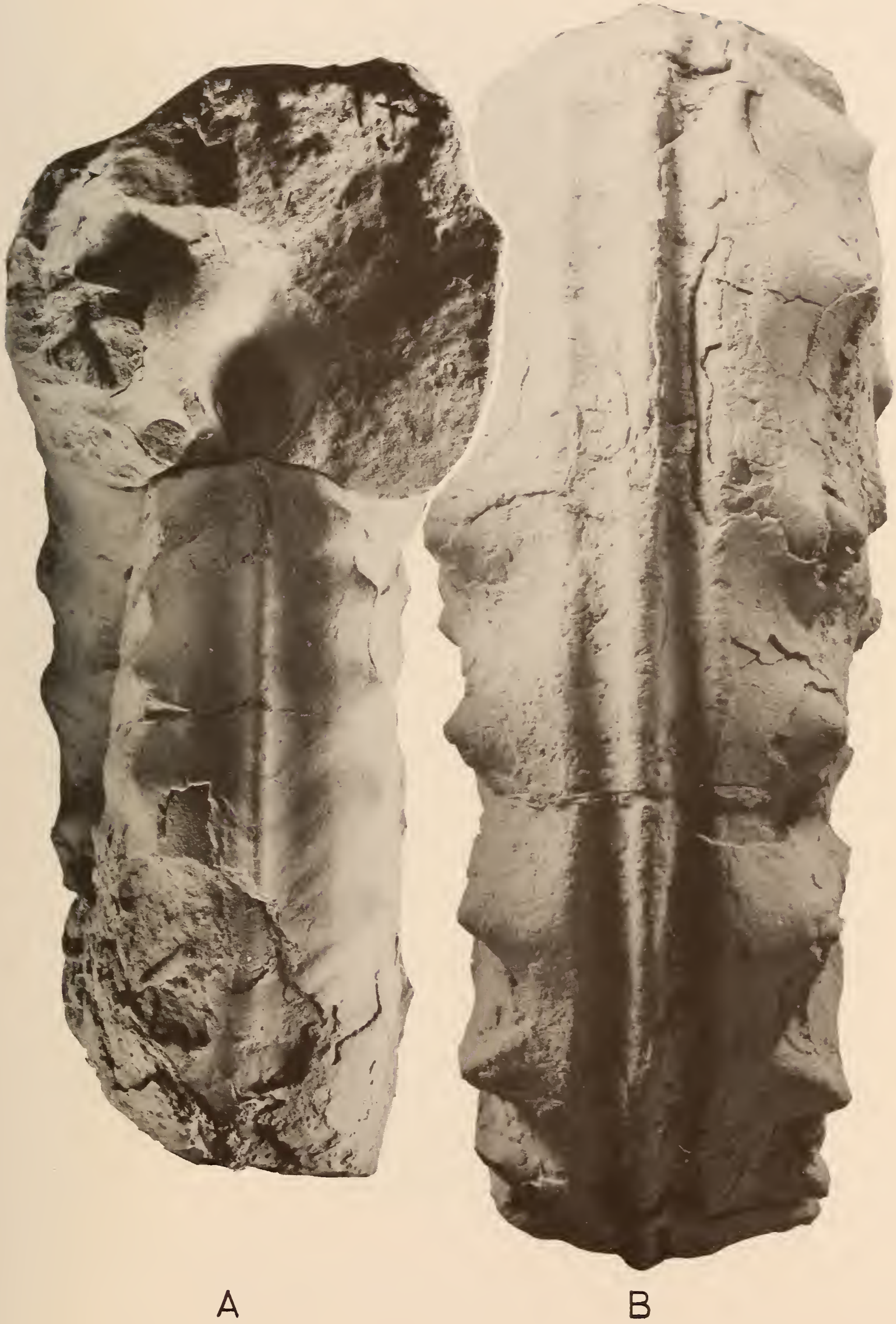

Fig. 117. *Gauthiericeras listeri* (van Hoepen, 1965). A. SAS Z342, inner whorls of paratype of *Falsebayites peregrinus* van Hoepen. × 1. B. SAS Z754, inner whorls of holotype of *G. listeri*. × 2.

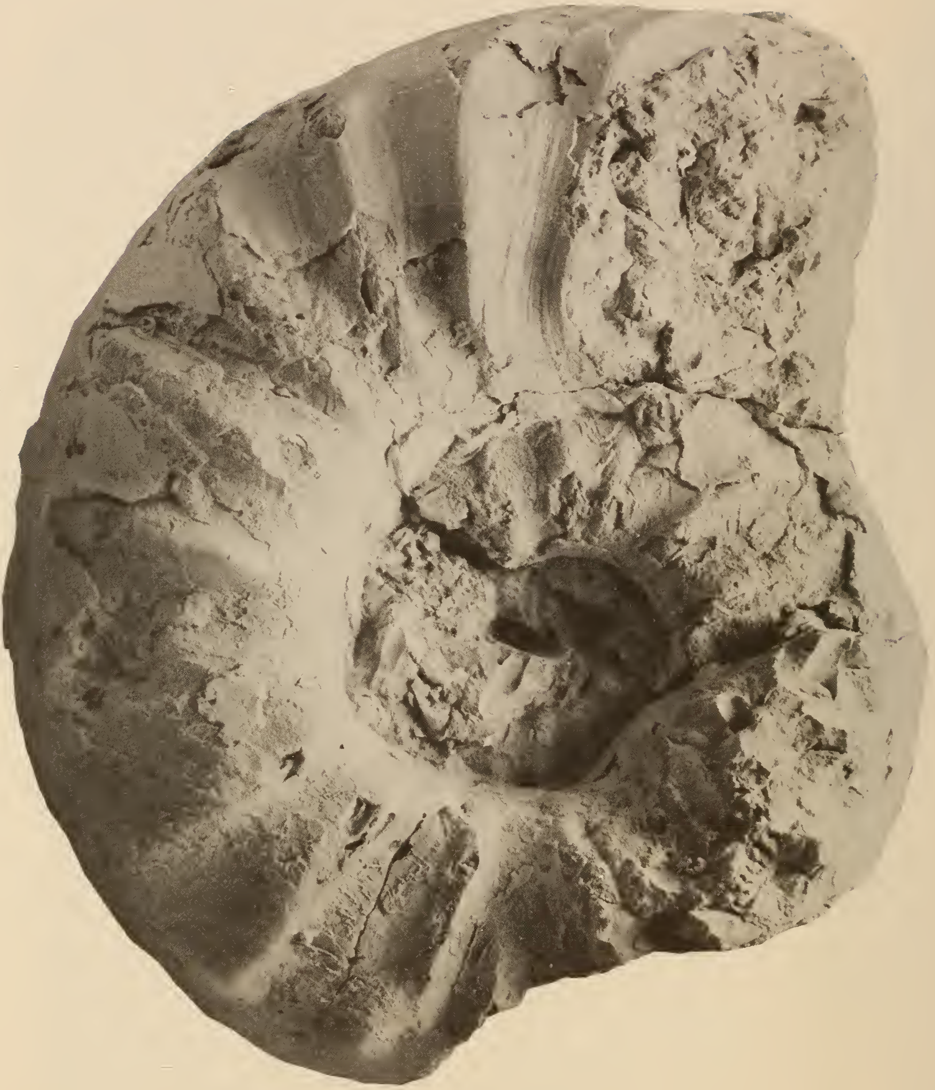

Fig. 118. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z342, paratype of Van Hoepen's *Falsebayites peregrinus*. × 0,64.

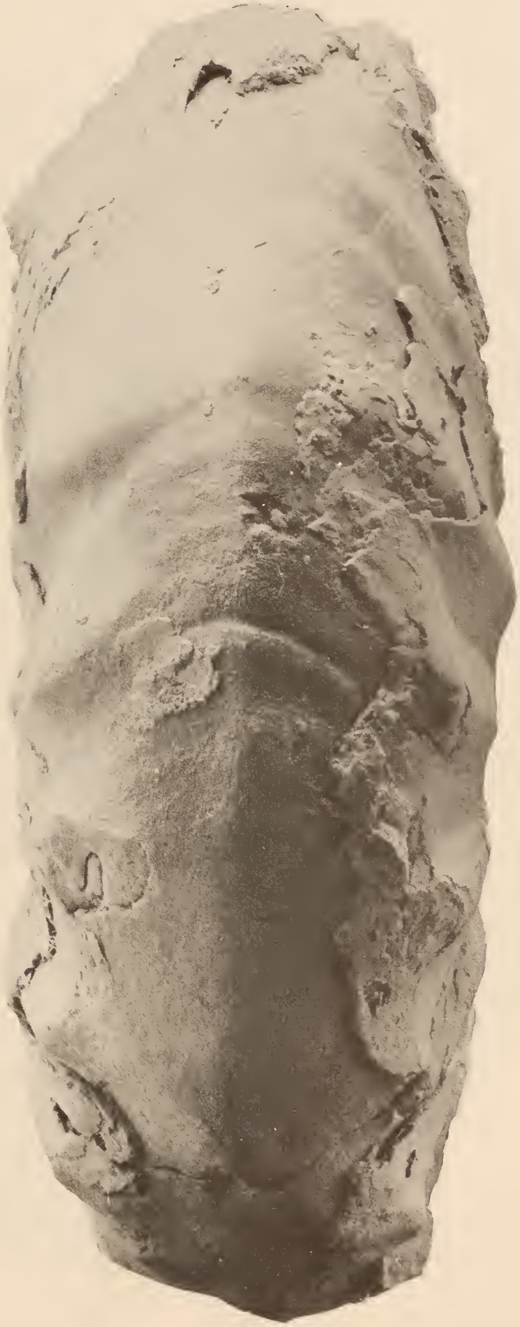

Fig. 119. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z342, paratype of Van Hoepen's *Falsebayites peregrinus*; section on body chamber showing fastigiate venter and slight constriction. × 1.

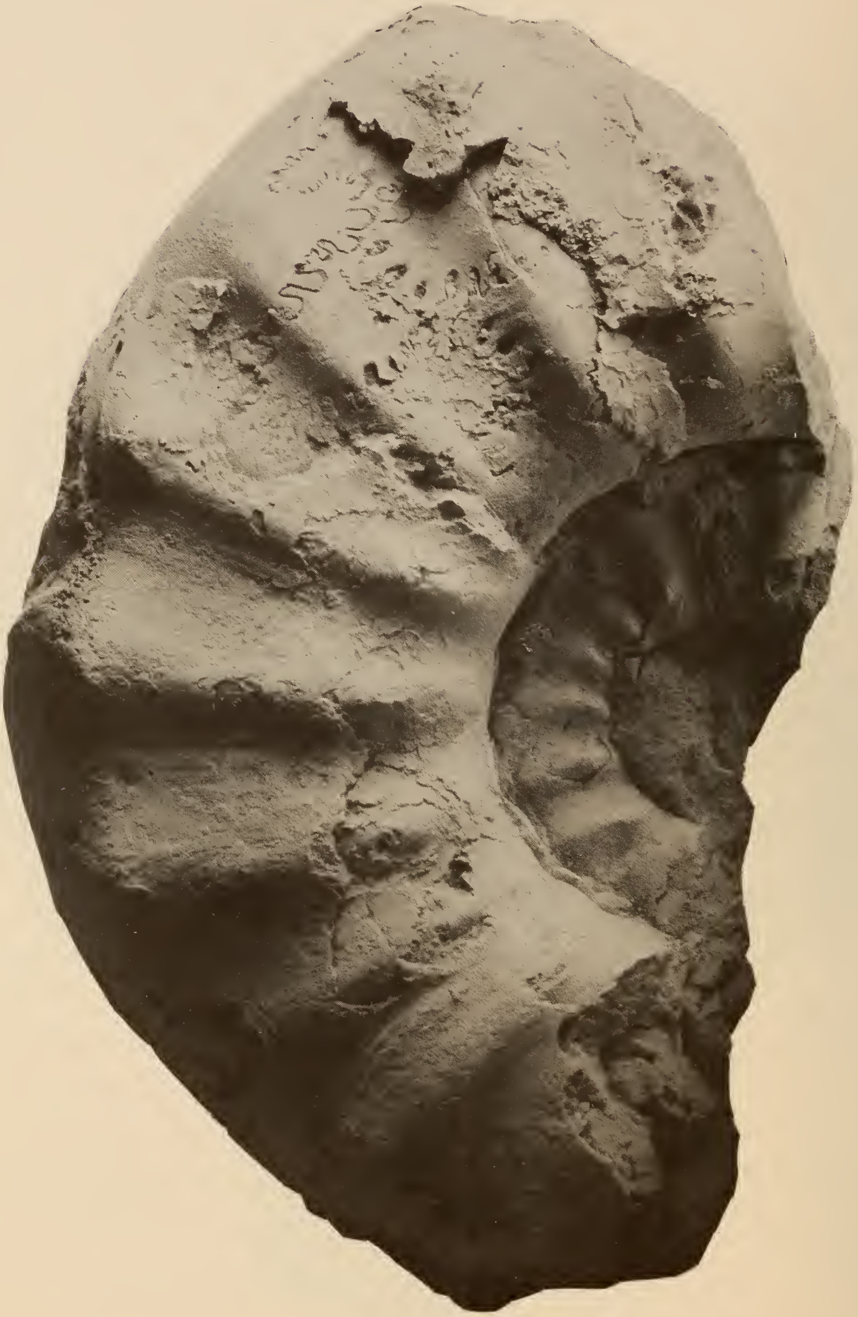

Fig. 120. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z341, holotype of Van Hoepen's *Falsebayites peregrinus*. × 1.

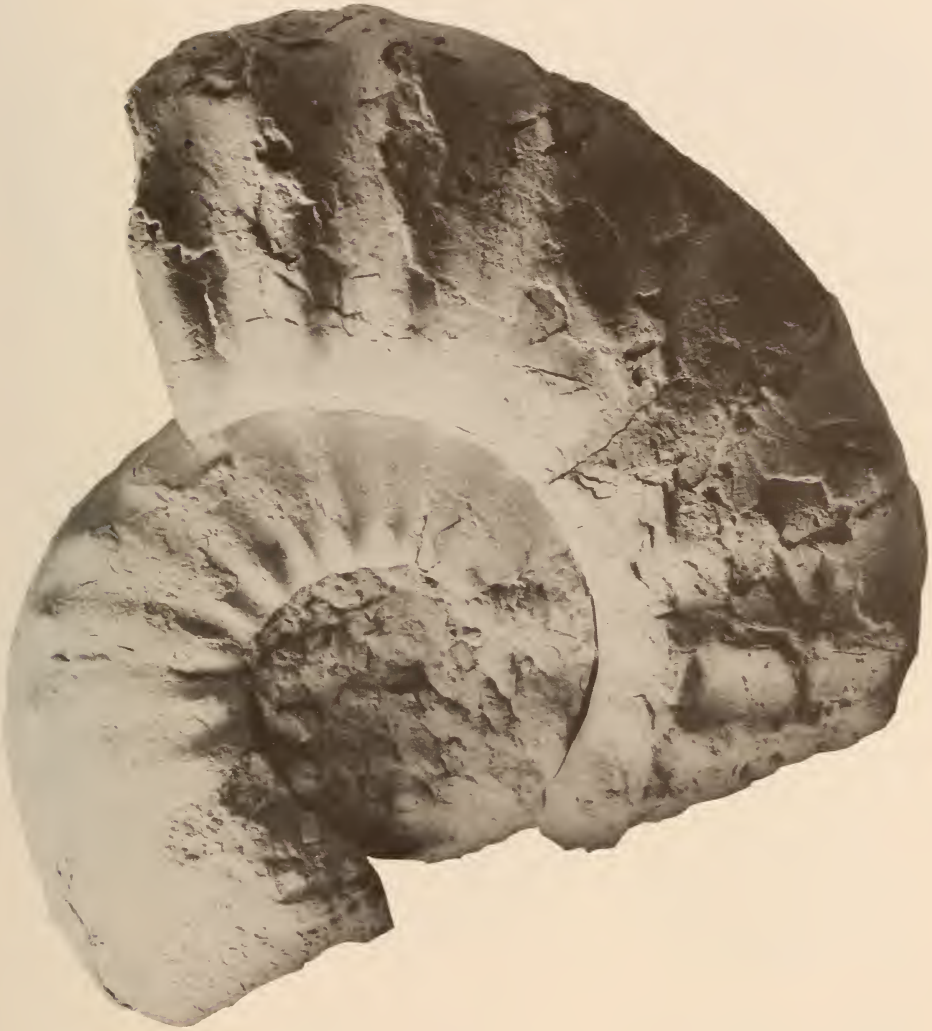

Fig. 121. *Gauthiericeras listeri* (van Hoepen, 1965). SAS Z755. Holotype of Van Hoepen's *Hluhluweoceras fugitivum*. × 0,71.

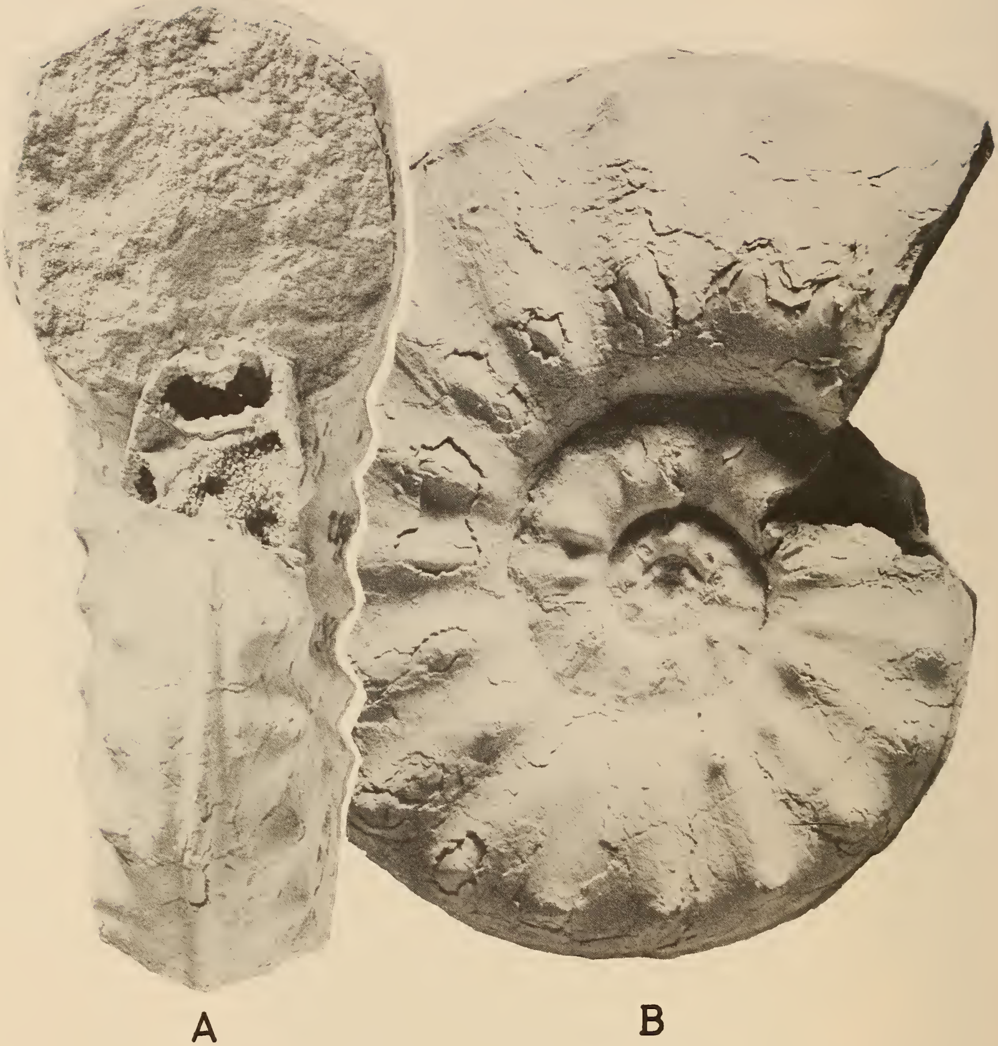

Fig. 122. *Gauthiericeras listeri* (van Hoepen, 1965). SAS H206/2, specimen showing early whorls. × 1.

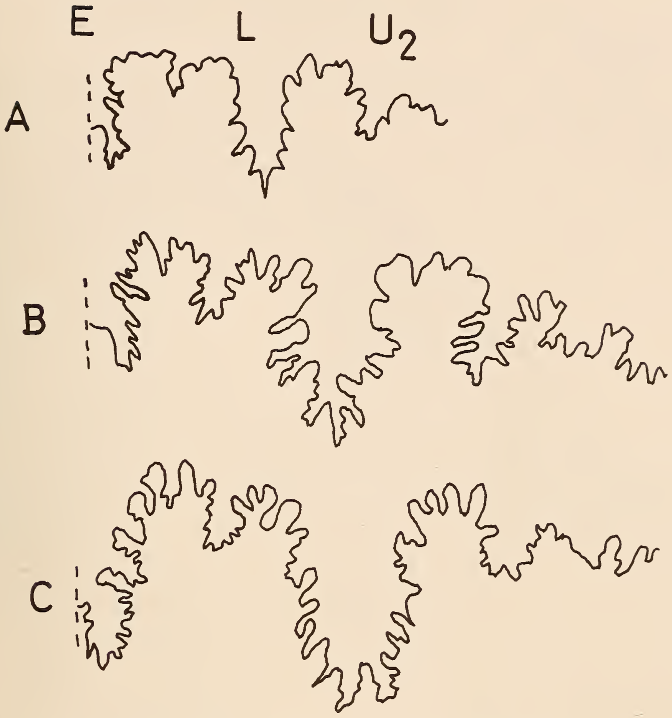

Fig. 123. *Gauthiericeras listeri* (van Hoepen, 1965). Suture-lines of Z755, Z754, Z341. × 1. (After Van Hoepen 1965, figs 8a–b, 9g.)

The venter is distinctly unicarinate, with a single, strong central keel bounded on either side by a depression of variable strength. The ribs often continue beyond the ventrolateral tubercle to the area of these depressions, thus creating the impression of wavy lateral keels, but these are not true keels.

Adult ornament is very variable as the figures show, but differences are all within bounds of specific variation. It ranges from weak (SAS Z755) (Fig. 121) through fairly well developed (as in SAS Z341) (Fig. 120) to very strong (SAS Z754) (Fig. 116).

A large part of the body chamber is preserved in SAS Z342, occupying about three-quarters of a whorl. At the apertural end of this specimen the ribs become increasingly prorsiradiate, the central keel less prominent, and prorsiradiate striae cross the venter (Fig. 119).

Suture-lines are shown in Figure 123A–C.

Discussion

The species as here interpreted comprises virtually the whole of Van Hoepen's subfamily Gauthiericeratinae and includes the type species of his 'genera' *Andersonites, Hluhluweoceras*, and *Falsebayites*. This species is probably derived from *G. obesum* through reduction of the umbilical width and increase in rate of whorl expansion.

'Andersonites' listeri is the most strongly ornamented morphological variant of the species and the inner whorls are somewhat reminiscent of *Peroniceras (P.) subtricarinatum* as far as lateral ornament is concerned. The venter, however, is distinctly unicarinate, and not tricarinate as stated by Van Hoepen (1965: 29) (Fig. 117B). There is only one central keel with a spiral furrow on either side. A slight extension of the lateral ribs to these depressions creates the appearance of wavy lateral keels. This together with imperfect shell preservation, probably led Van Hoepen to believe that the specimen was tricarinate.

'Hluhluweoceras' fugitivum (Fig. 121) has massive quadrate inner whorls with weak lateral ornament, but can be connected to *G. listeri* by transitional forms, so that separation is artificial.

'Falsebayites' peregrinus (Figs 117A, 118–119) the only species in Van Hoepen's subfamily Gauthiericeratinae based on more than one specimen, shows a very rapid increase in whorl height and an umbilical diameter of only 32 per cent. The general pattern of ornament, however, is that of *G. listeri*.

Collignon (1965: 49, pl. 435 (fig. 1797)) reported a species from the Middle Coniacian of Madagascar *G. listeriforme*, that is very much like *G. listeri*. The whorl section is much wider than high, the whorl breadth to height ratio being 1,12. It, too, is a synonym of *G. listeri*.

Occurrence

In Zululand well-dated specimens are restricted to Coniacian IV. The Madagascan specimen referred to the species is said to be from the 'Coniacian Moyen'.

Gauthiericeras album (van Hoepen, 1965)

Figs 124–126

Fluminites albus van Hoepen, 1965: 31, pl. 24, text-fig. 9c–e.

Type specimen

The holotype is SAS Z757 (Fig. 124) from localities 91 or 92 near the estuary of the Hluhluwe River, Zululand, St. Lucia Formation, Coniacian IV or V.

Material

BMNH C83792 is from locality 83 and is precisely localized as Coniacian IV. A more complete specimen, SAS Z871, is from the same locality and horizon as the holotype.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z871	243,0	69,0(28,4)	86,0(35,4)	0,80	86,0(35,4)	17:17
Z757	—	31,0	40,0	0,77		

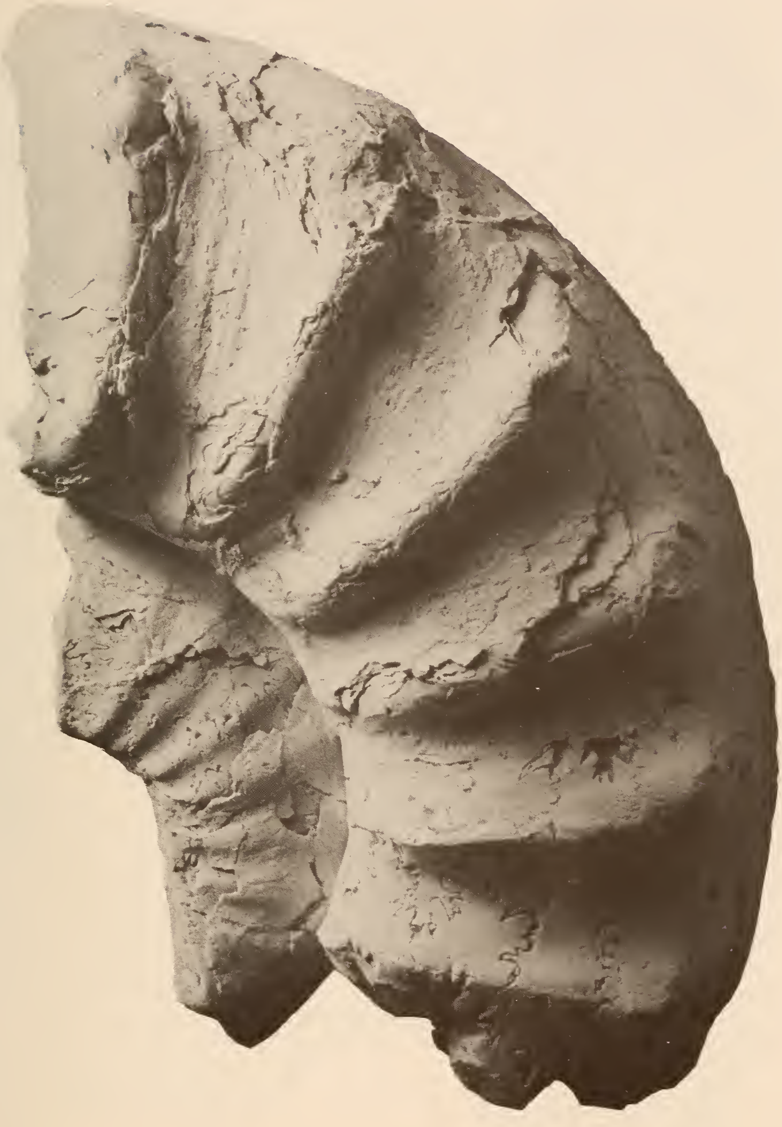

Fig. 124. *Gauthiericeras album* (van Hoepen, 1965). Holotype SAS Z757. × 1.

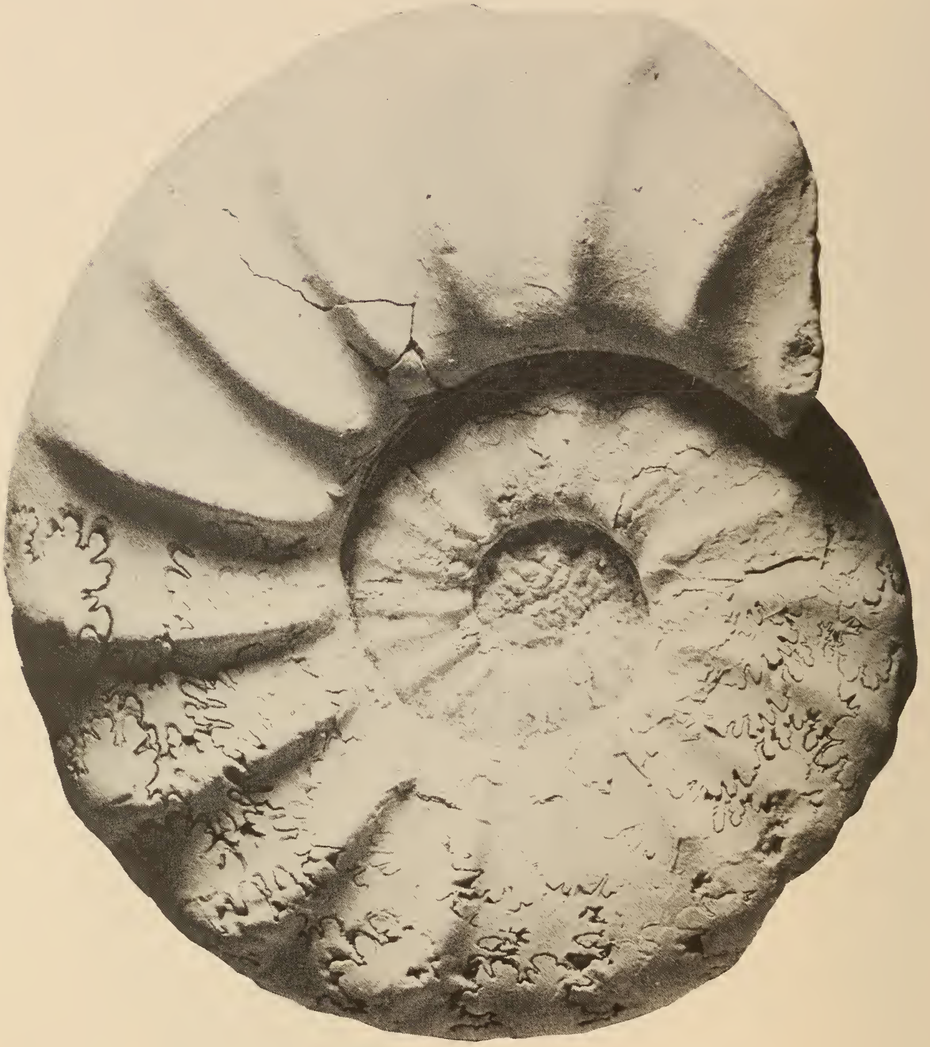

Fig. 125. *Gauthiericeras album* (van Hoepen, 1965). SAS Z871. × 0,56.

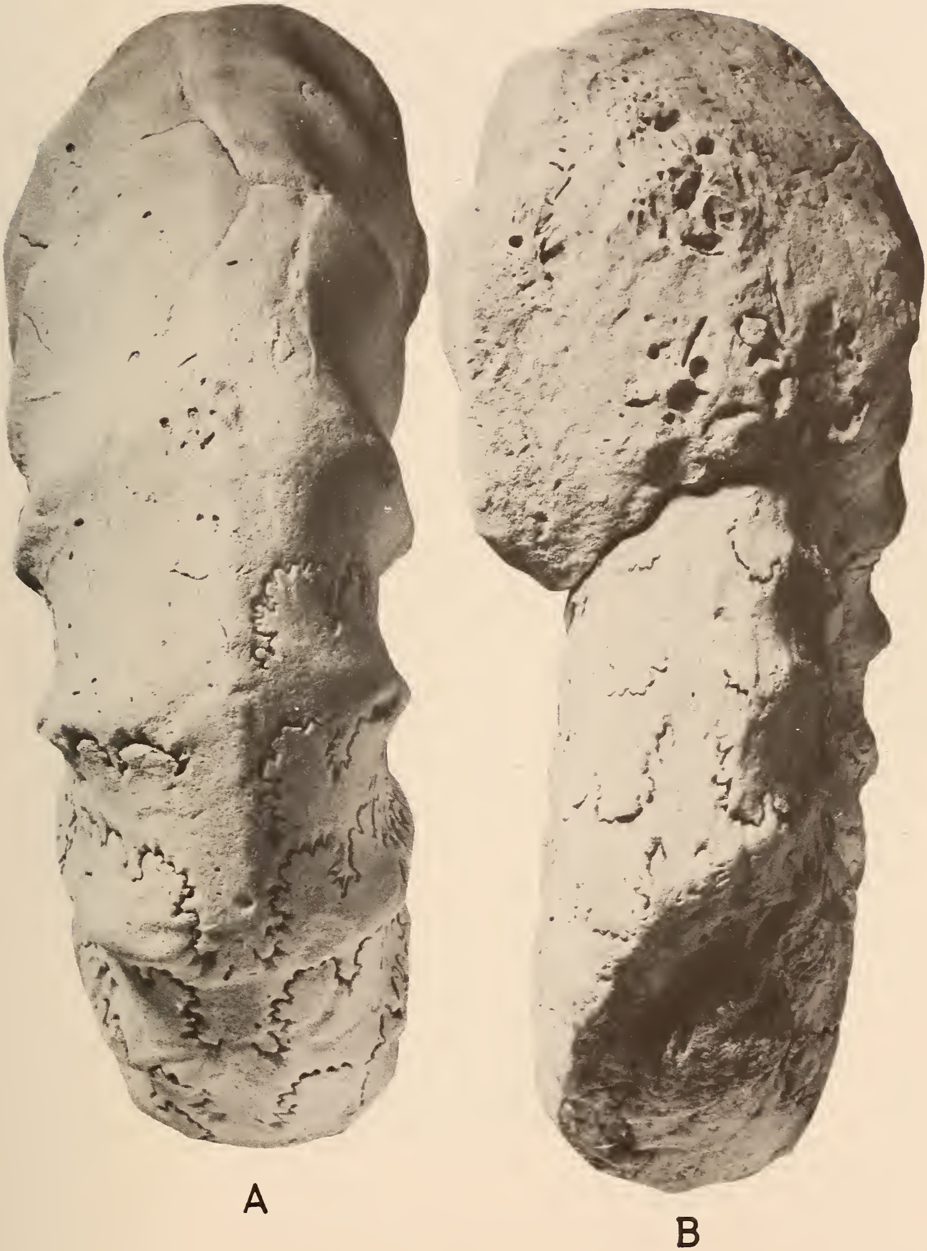

Fig. 126. *Gauthiericeras album* (van Hoepen, 1965). SAS Z871. × 0.65.

Description

Coiling is moderately involute, with an umbilical diameter of 35 per cent in the only complete specimen available. The whorl section is ovoid throughout ontogeny, compressed, with little-inflated flanks (the maximum width at mid-flank), and a broadly rounded venter. The umbilical wall is gently rounded.

Ornament on the inner whorls of the holotype is very weak, consisting of umbilical bullae, prorsiradiate ribs and ventrolateral clavi. The venter appears tricarinate, but this is a result of the strong development of depressions on either side of the keel. On the outer whorls ornament strengthens considerably. The ribs become sharp-crested and widely spaced, whereas the umbilical tubercles become progressively radially elongated and eventually merge with the ribs. The ventrolateral tubercles similarly merge with the ribs, giving the latter a club-like appearance. Part of the body chamber is preserved in SAS Z871 (Fig. 125) and here adult ornament is fully developed.

Discussion

Unfortunately this species is poorly represented in numbers, so that the range of intraspecific variation cannot be established. It is easily distinguished from *G. obesum* by the ovoid, rather than quadrate to rectangular whorl section of the latter. The outer whorls of *G. listeri* are remarkably similar to those of *G. album*, but, again, the whorl section of the former is more quadrate.

Occurrence

Coniacian IV of Zululand.

Gauthiericeras albiforme sp. nov

Figs 127–129

Type specimens

The holotype is SAS 92/4 (Figs 127–128) from between localities 83 and 84, near Picnic Point, False Bay, Zululand, St. Lucia Formation, Coniacian V. Paratypes are SAS 92/2–3, from the same locality and horizon as the holotype.

Dimensions

	D	Wb	Wh	Wb/Wh	U	R
92/3	113,0	36,0(31,9)	48,0(42,5)	0,75	30,0(26,6)	—
92/2	160,0	48,0(30,0)	58,0(36,2)	0,83	55,0(34,4)	—
92/4	181,0	61,0(33,7)	72,0(39,8)	0,85	62,0(34,2)	19:20

Description

The umbilicus is narrow in the early growth stages, comprising only 27 per cent of the diameter, but increases to about 34 per cent in larger individuals. In adults the whorl section is distinctly subtrigonal, with an overhanging umbilical wall and little-inflated flanks converging to a narrow, unicarinate venter.

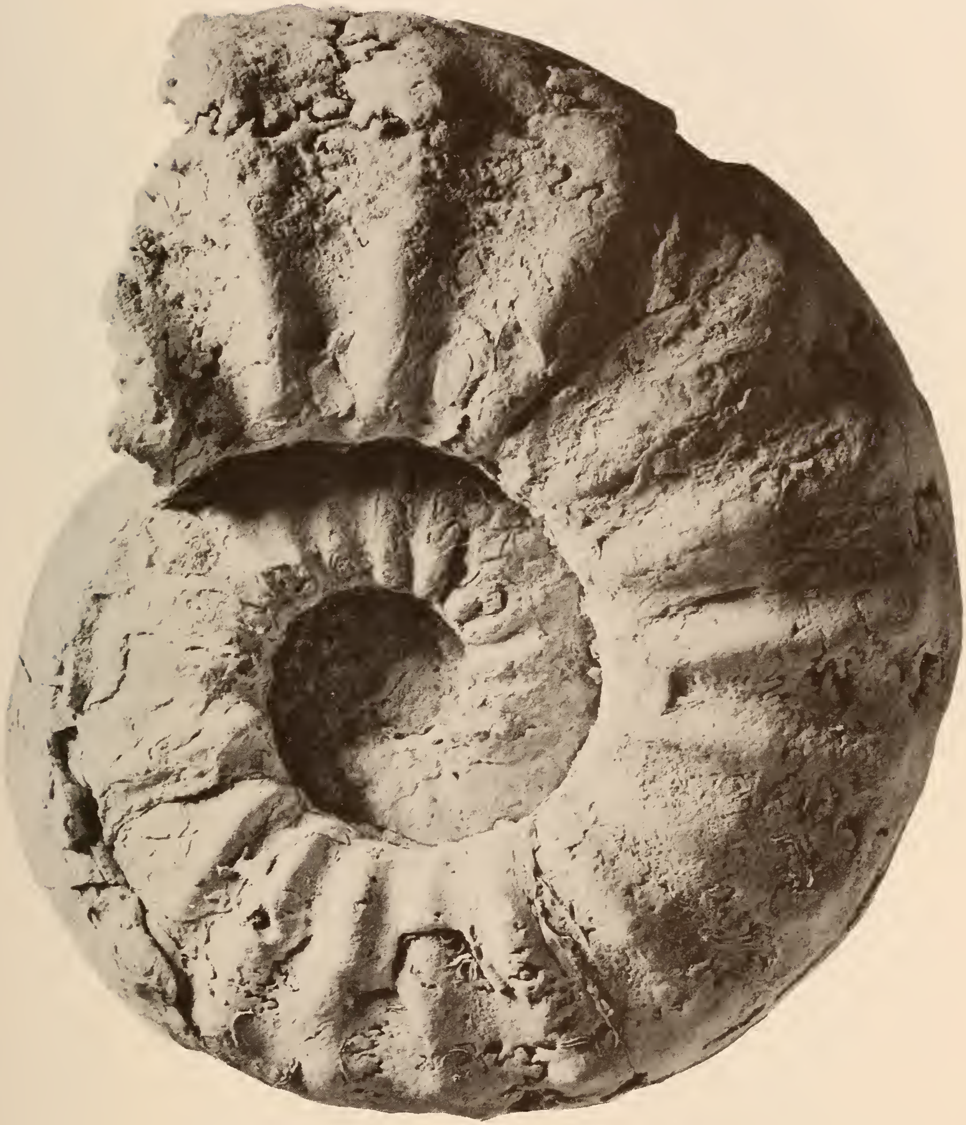

Fig. 127. *Gauthiericeras albiforme* sp. nov. Holotype SAS 92/4. × 0,86.

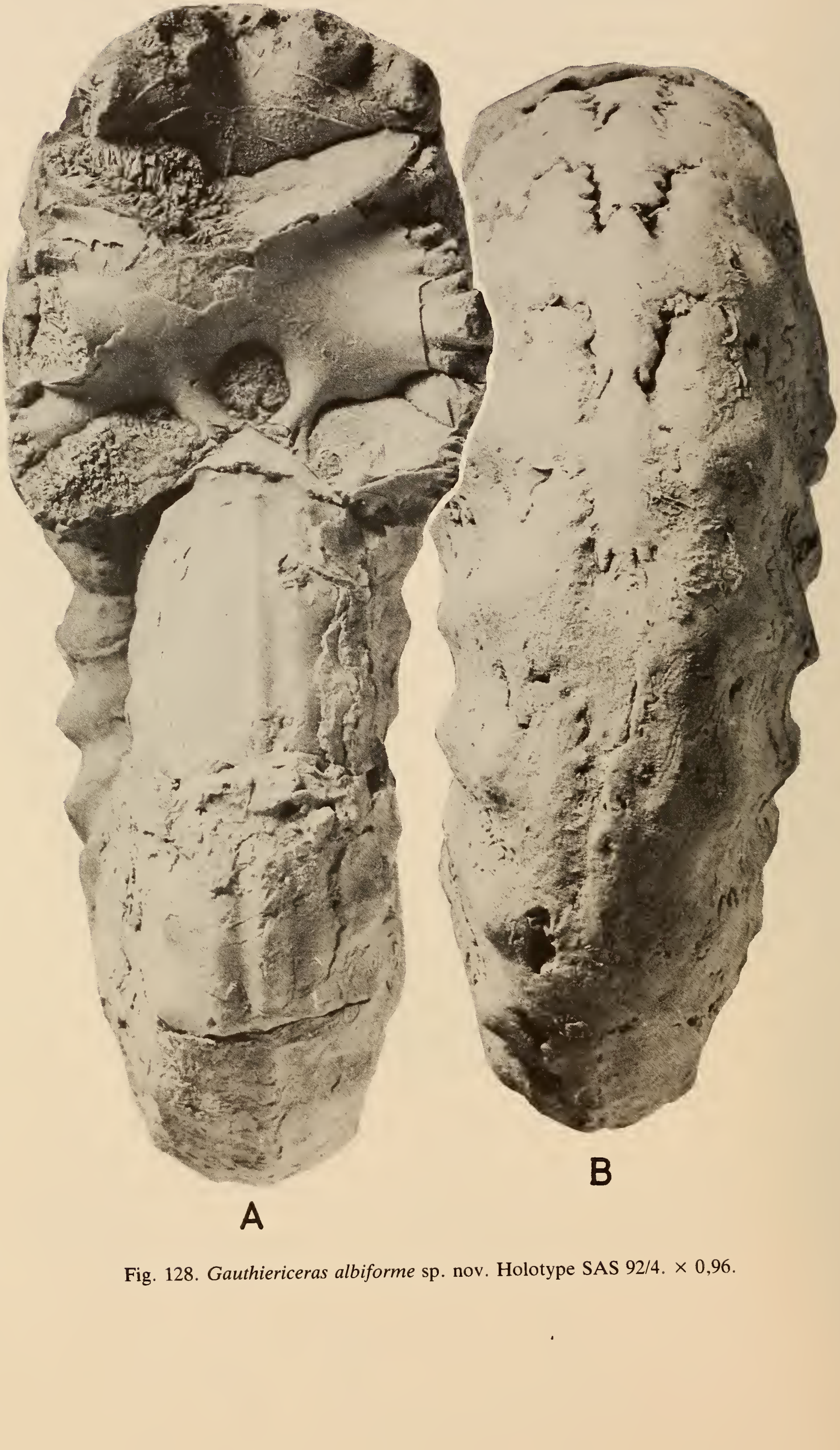

Fig. 128. *Gauthiericeras albiforme* sp. nov. Holotype SAS 92/4. × 0,96.

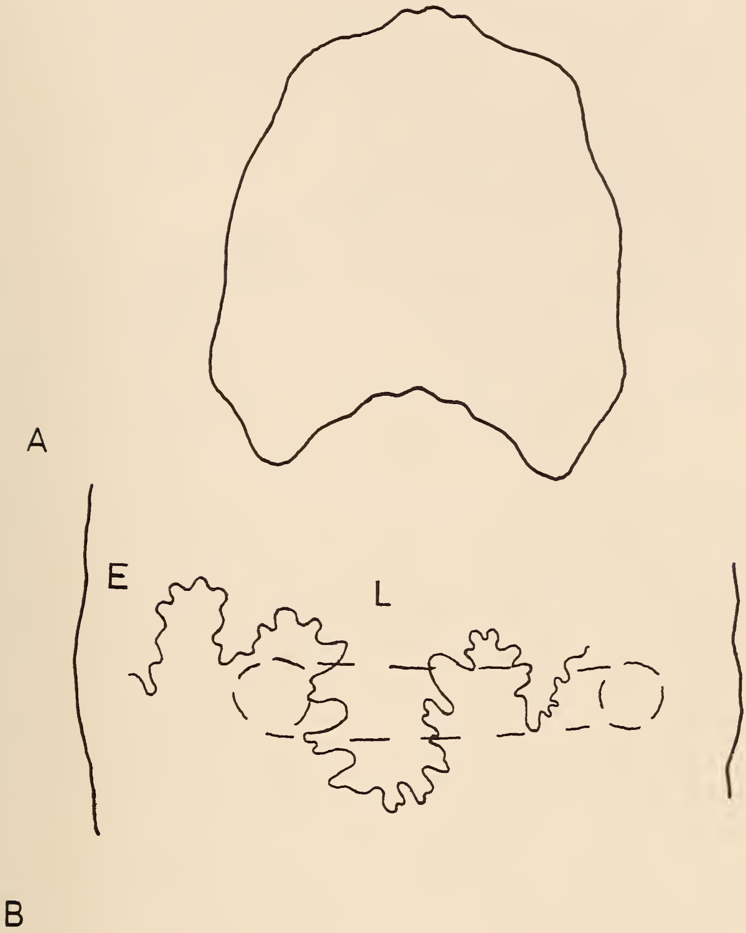

Fig. 129. *Gauthiericeras albiforme* sp. nov. Whorl section and suture-line. × 0,5.

Ornament throughout consists of distinctly pinched, auricular umbilical bullae that merge into strong, more or less radial or slightly prorsiradiate concave ribs. These terminate in indistinct ventrolateral tubercles. On the outer whorls ribbing is generally single, but on the inner ones bifurcations may occur at the umbilical tubercle. Rib density is 19 to 20 on the outer whorls.

The venter is distinctly unicarinate, with only shallow spiral depressions on either side of the keel.

Discussion

Distinguishing features of this species are the narrow umbilicus and the subtrigonal whorl section with an overhanging umbilical wall. As far as ornament is concerned, there is great similarity to *G. album*, described above. Although the material is limited, it may be possible to derive *G. albiforme* from *G. album* through slight decrease in umbilical diameter and increasing rate of whorl expansion. Given enough material connecting the two species, separation at subspecific level would probably be sufficient.

The subtriangular whorl section serves to distinguish the species from *G. obesum* and *G. listeri.*

Occurrence

Upper Coniacian of Zululand. This appears to be the last surviving species of *Gauthiericeras.*

Gauthiericeras libertae van Hoepen, 1955

Figs 130–134

Gauthiericeras libertae van Hoepen, 1955: 372, figs 23–25.
Gauthiericeras planulatum van Hoepen, 1955: 374, figs 29–31.

Type specimens

The holotype of *Gauthiericeras libertae* is SAS Z4 (Figs 132–134), it was found by Van Hoepen in a pile of rubble probably at locality 91 or 92 of Kennedy & Klinger (1975) near the Hluhluwe estuary, Zululand, St. Lucia Formation, probably Coniacian IV. The holotype of *G. planulatum* is SAS Z3, also from near the Hluhluwe estuary close to locality 89 or 90 of Kennedy & Klinger, St. Lucia Formation, probably Coniacian IV.

Material

SAS Z1136, from locality 73, degraded river cliffs and stream exposures on the Mzinene River downstream from the junction with the Munywana, Zululand, St. Lucia Formation, Coniacian IV or V. SAS H205/22 is from locality 90, SAS H205/1 from locality 90 or 91, both near the Hluhluwe estuary, Zululand, Coniacian IV or V. SAS Z2018 and BMNH C83797–C83799 from locality 83, foreshore exposures at Mason's Camp, Zululand, St. Lucia Formation, Coniacian IV.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Z2018	131,0	41,0(31,3)	52,0(39,7)	0,79	48,0(36,6)	22:22
Z3	134,0	37,0(27,6)	51,0(38,1)	0,72	46,0(34,3)	18:21
H205/22	135,0	37,0(27,2)	49,0(36,0)	0,75	53,0(38,9)	—
Z1136	137,0	43,0(31,4)	50,0(36,5)	0,86	50,0(36,5)	—
H205/1	148,0	41,0(27,7)	53,0(35,8)	0,77	54,0(36,5)	16:16
Z4	150,0	40,0(26,7)	54,0(36,0)	0,74	55,0(36,7)	17:30

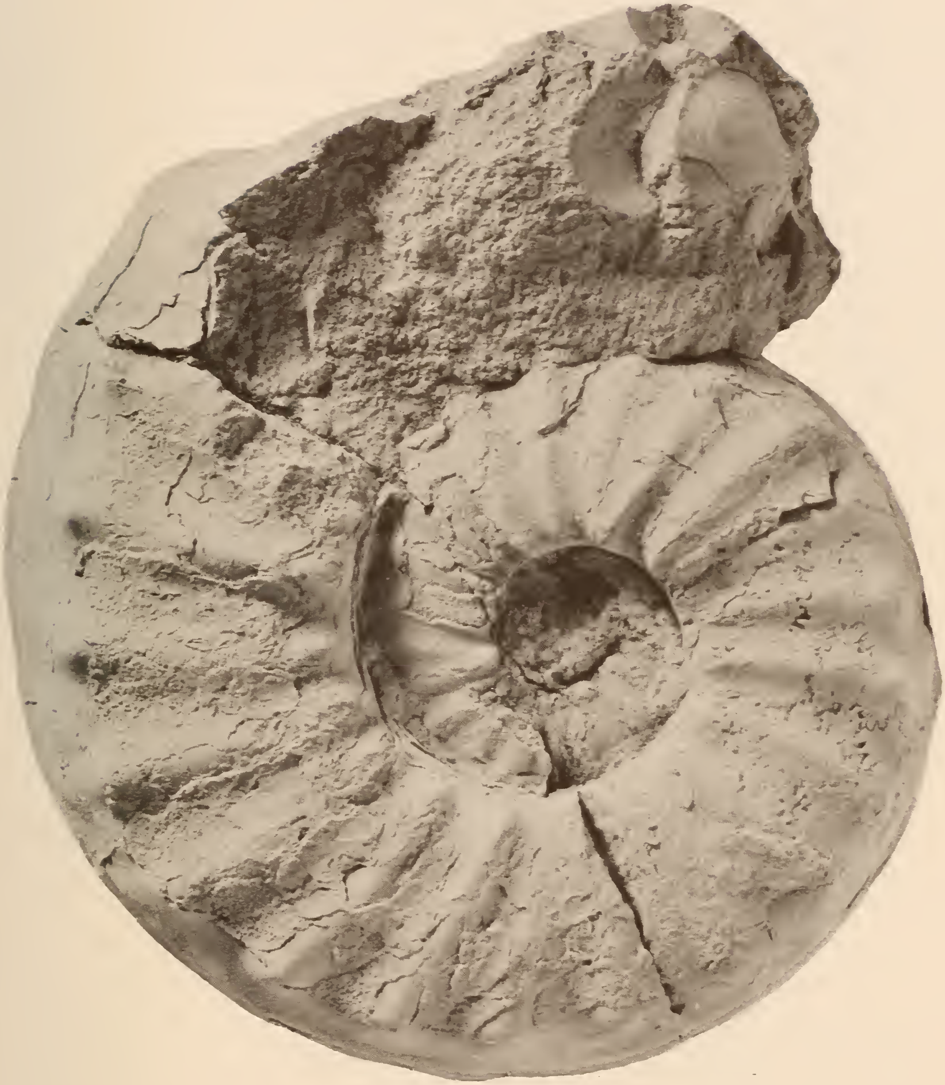

Fig. 130. *Gauthiericeras libertae* van Hoepen, 1955. SAS Z3 holotype of *G. planulatum* van Hoepen, 1955. × 0.96.

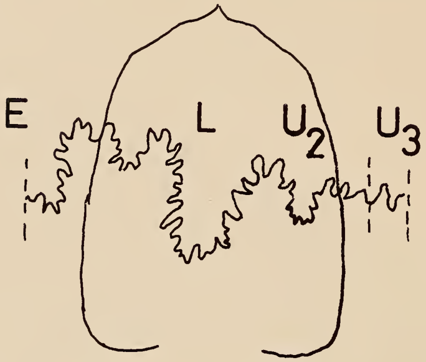

Fig. 131. *Gauthiericeras libertae* van Hoepen, 1955. Whorl section and suture-line of the holotype of *G. planulatum*. × 1. (After Van Hoepen 1955, figs 30–31.)

Description

Coiling is evolute, the umbilical diameter varying between 34 and 38 per cent of the total diameter, with successive whorls overlapping to the ventral tubercle or a little beyond, so that about 25 per cent of the previous whorl is covered. The whorl section is compressed throughout, with whorl breadth to height ratios that vary between 0,72 and 0,86. The inner flanks are gently rounded, the outer flanks flattened and subparallel or slightly convergent, the venter narrow and fastigiate.

There are 16 to 22 weak to prominent umbilical bullae per whorl. These give rise to either single ribs or pairs of ribs that vary from weak to strong between individuals but are straight and prorsiradiate to mid-flank and curve slightly forward to terminate in weak ventral clavi. The ribs are prolonged forward to the edge of a shallow groove that flanks a blunt undulating siphonal keel. The outer edges of the grooves are also undulose, giving an appearance of incipient lateral keels.

Suture simple, as in other members of the genus (Figs 131, 134).

Discussion

Van Hoepen separated *Gauthiericeras libertae* and *G. planulatum* on the basis of the predominance of single ribs in *libertae* and the predominance of paired ribs in *planulatum*, as well as sutural details. New material shows that there is variation in this respect, and the common features of overall shell form and the distinctive ventral ornament with crenulate siphonal keel and crenulate edges to the flanking grooves suggest that only a single species is present.

Ribbing style, evolute coiling combined with compressed whorls and the distinctive venter distinguish this species from all others.

Occurrence

Coniacian IV of Zululand.

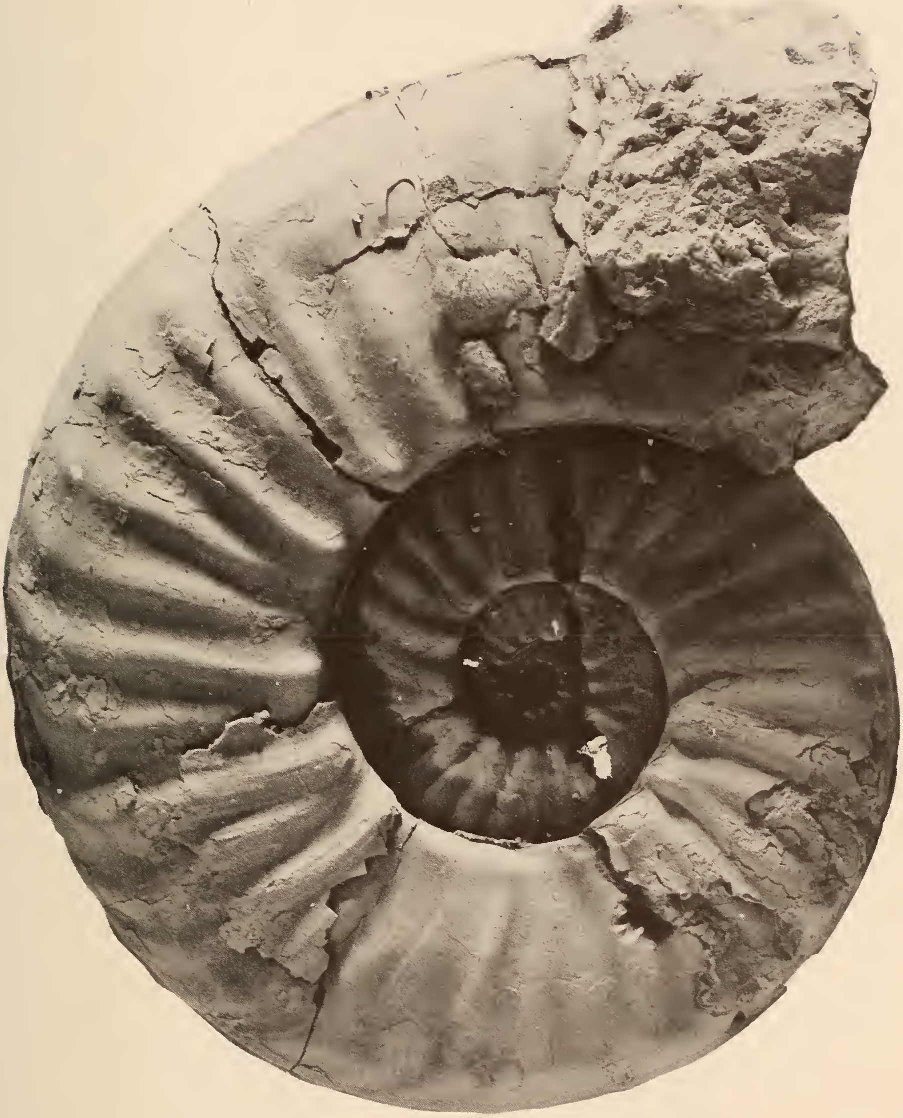

Fig. 132. *Gauthiericeras libertae* van Hoepen, 1955. Holotype SAS Z4. × 0,85.

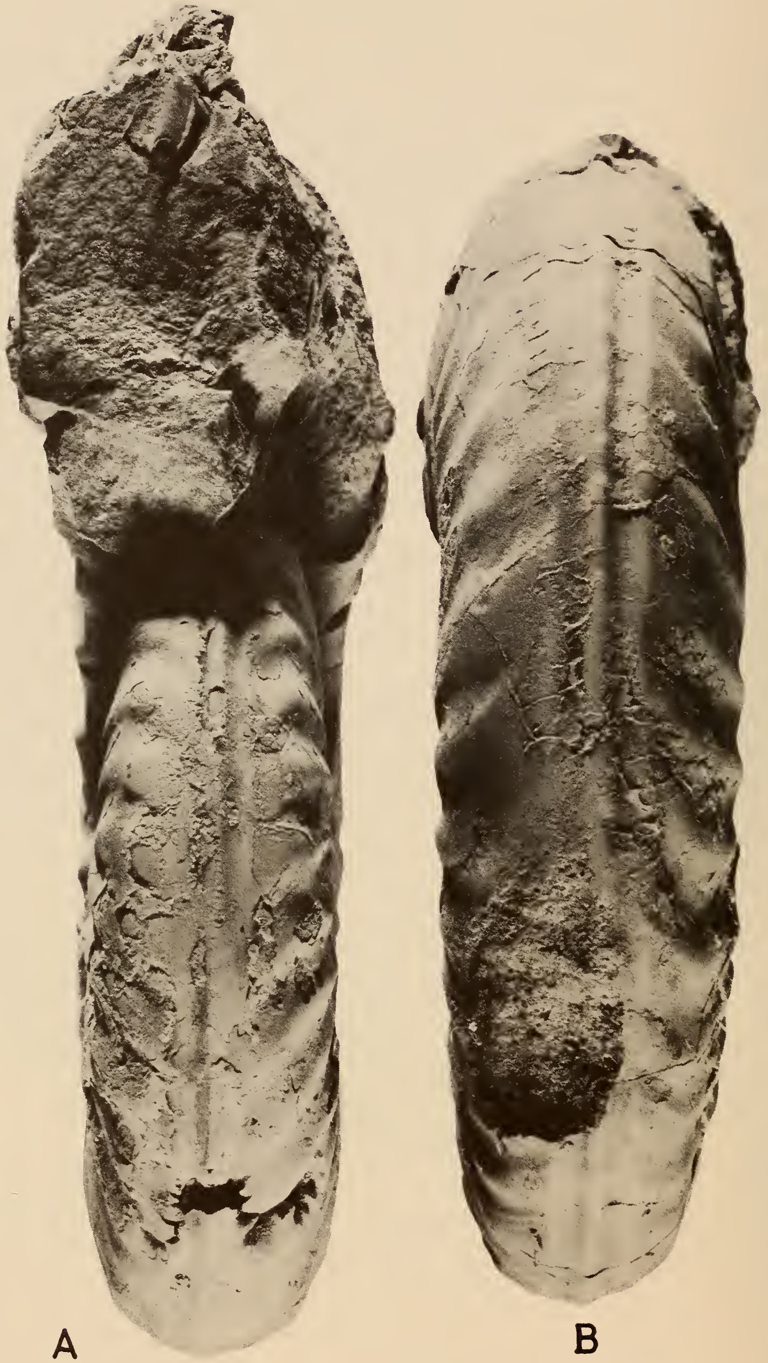

Fig. 133. *Gauthiericeras libertae* van Hoepen, 1955. Holotype SAS Z4. × 1.

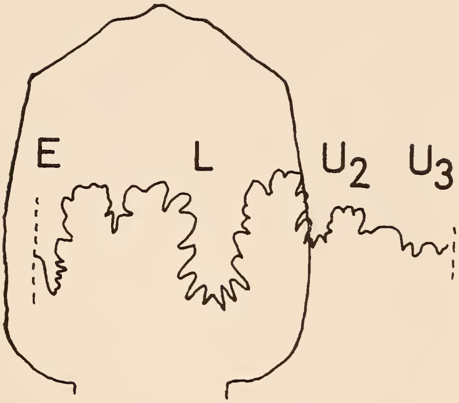

Fig. 134. *Gauthiericeras libertae* van Hoepen, 1955. Whorl section and suture-line of holotype. × 1. (After Van Hoepen 1955, figs 24–25.)

CONCLUSIONS

A general reappraisal of Coniacian stratigraphy and revision of the very rich peroniceratid faunas found in Zululand provide an outline of the evolution of the group that is of some significance for interregional correlation and elucidation of evolutionary patterns among late Cretaceous ammonites (Fig. 135).

The earliest genus of the Peroniceratinae is *Peroniceras* itself. The appearance of *P. (Peroniceras)* (of which *Fraudatoroceras* van Hoepen, 1965, *Cobbanoceras* Matsumoto, 1965, and *Gloriaceras* Etayo-Serna, 1979, are synonyms) marks the base of the Middle Coniacian as that term is used here. There is a hiatus in the record between the first appearance of *Peroniceras* and the Collignoniceratinae, which are believed to be the ancestral stock spanning the Lower Coniacian. Matsumoto (1965: 213) believed that the origin of *Peroniceras* lay in *Prionocyclus*, and the *Prionocyclus* lineage certainly survived to give rise to *Prionocycloceras*, which extends to the Upper Coniacian. Matsumoto suggested that the lateral keels of *Peroniceras* arose by the elevation of the outer edges of the grooves flanking the keel of ancestral *Prionocycloceras*. Independent observations by Etayo-Serna (1979) and the present authors shows that the keels arise by elongation and eventual absorption of outer ventrolateral clavi into a keel, and that both lateral and siphonal keels of several *Peroniceras (Peroniceras)* species show undulations at some stage in ontogeny.

The suture of the type species of *Peroniceras (Peroniceras)*, *P. (P.) moureti* de Grossouvre, 1894 (a synonym of *P. (P.) tridorsatum* (Schlüter, 1867)) is relatively simple, like that of ancestral Collignoniceratinae. Other species, such as *P. (P.) dravidicum* Kossmat, 1895, have a much more complex suture, with long, narrow and finely indented saddles. Evolution must have been from the simple *P. tridorsatum* type to complex *P. dravidicum* type, although there is no

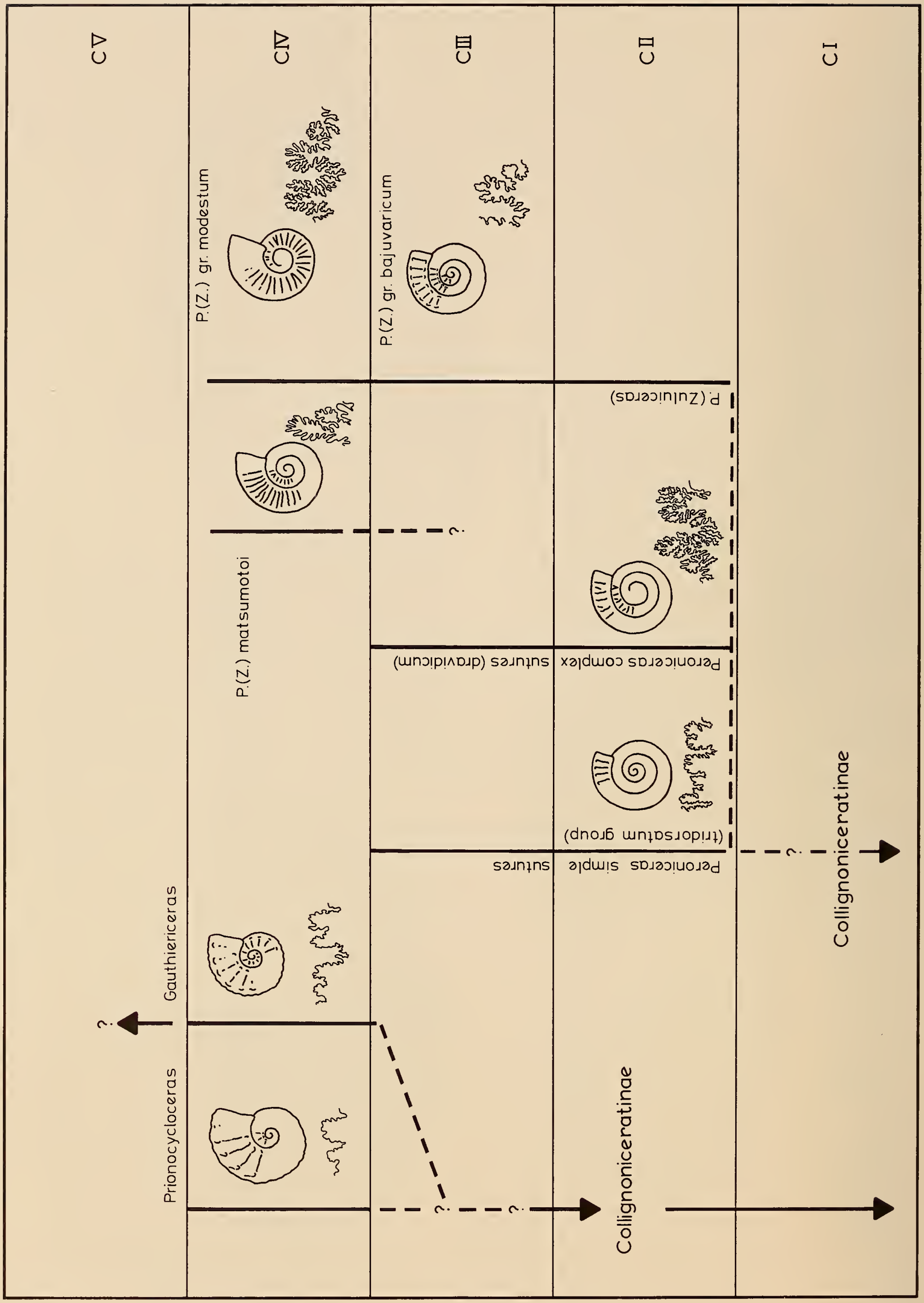

Fig. 135. Suggested phylogenetic relationships within the subfamily Peroniceratinae.

detailed stratigraphy to support this. In Zululand, *P. (Peroniceras)* of both types are confined to the Middle Coniacian. Only in Japan is there a suggestion that *P. (Peroniceras)* extends above this and into the Santonian; however, the supporting evidence is not wholly convincing.

Peroniceras (Zuluiceras) van Hoepen, 1965 (of which *Zuluites* van Hoepen, 1965, and *Sornayceras* Matsumoto, 1965, are synonyms) also appears in the Middle Coniacian, with some slight evidence (in Zululand at least) that it slightly post-dates the nominate subgenus. It has a relatively complex suture of *P. dravidicum* type. The earliest species are relatively evolute, but through the higher Middle and lower Upper Coniacian there is a trend towards increasing involution, compression of the whorls, and loss of ornament.

Gauthiericeras (of which *Ciryella* Wiedmann, 1960, *Fluminites* van Hoepen, 1965, *Andersonites* van Hoepen, 1965, *Hluhluweoceras* van Hoepen, 1965, and *Falsebayites* van Hoepen, 1965, are synonyms) appears at the base of the Upper Coniacian in Zululand. Only the cryptic diminutive '*Schloenbachia*' *boreaui* de Grossouvre, 1894, which may appear in the Middle Coniacian in France, points to a possible slightly earlier appearance. The genus shows much stronger similarities to *Prionocycloceras* than to other, earlier Peroniceratinae, and this is believed to be its origin. Both evolute and involute species occur in the fourth division of the Zululand Coniacian, but there is insufficient evidence to allow interpretation of this in terms of an evolutionary trend as has been demonstrated in the *Peroniceras* → *Zuluiceras* series through the Middle and Upper Coniacian. *Ishikariceras* Matsumoto, 1965, with its evolute strongly ornamented inner whorls with strong umbilical and ventral tubercles, a strong siphonal keel flanked by weak grooves, and an almost smooth body chamber, appears to be a distinct genus. Its precise horizon within the Coniacian is unknown. If, as appears likely, the two known specimens are adult, it is a micromorph.

Neogauthiericeras Collignon, 1969, described from the Santonian–Campanian boundary of Madagascar, is, by virtue of its stratigraphic isolation from other Peroniceratinae, more likely to be a *Gauthiericeras* homoeomorph of texanitine affinities analogous to *Reginaites*, a texanitine homoeomorph of *Peroniceras*.

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